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SIZE VARIABILITY IN PLANKTIC FORAMINIFERS

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In nova fert animus mutatas dicere formas corpora

Mein Anliegen ist es, von Körpern zu erzählen,
die sich in Gestalten verschiedener Art verwandelt haben.

Ovid, Metamorphosen

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ABSTRACT

Planktic foraminifers are a major marine calcareous microfossil group. Their shells are abundant in most oceanic sediments. This unique pelagic sediment record of the deep sea was used to investigate macro-evolutionary changes in the test size of planktic foraminiferal assemblages, the impact of physical factors on morphological diversity and the biotic response to environmental perturbations. The pelagic sedimentary record is exceptionally complete, with global coverage available from well-dated deep-sea cores recovered by international drilling programs (DSDP, ODP).

Previous work has shown that test size of planktic foraminiferal species can be related to ecological factors such as temperature (Bé et al. 1973; Hecht 1976), upwelling intensity (Naidu and Malmgren 1995) and environmental variability (Bé and Duplessy, 1976; Naidu and Malmgren, 1995) (Chapter 1). In addition, it has been shown that test size changes during evolution (Malmgren et al., 1983; Corfield and Shackleton, 1988; Kucera and Malmgren, 1998). Most studies of evolutionary size changes in planktic foraminifers have focused on single species or lineages (e.g. Malmgren and Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato and Thierstein, 1997; Kucera and Malmgren, 1998; MacLeod et al., 2000).

This study rather focuses on changes in the entire planktic foraminiferal assemblages, which holds the potential of gaining insights into long-term macro- evolutionary processes. The maximum diameter of more than 1.6 million foraminifers was measured with an automated light microscope for three different data sets (Chapter 2). In each sample, the size spectrum of the entire assemblage was measured. Since size spectra are strongly skewed towards large size, the value separating the largest 5% from the smallest 95% of the assemblage was taken as an estimator for assemblage size changes and called assemblage size.

Ecological influences on size are identifiable in analyses of Holocene assemblages. The correlation between ecological changes and test size changes has been tested and confirmed in late Quaternary records. These new insights are used to interpret the Cenozoic planktic foraminiferal size record.

In the Holocene, geographical variations in the size distribution within the entire foraminiferal assemblage are related to environmental gradients, e.g. temperature and primary productivity, in the ocean (Chapter 3). Temperature-related effects, the main driving force behind assemblage size changes, results in an increase in size from polar to tropical biogeographic zones. However, this increase is not linear, and deviations are the result of secondary environmental factors such as primary productivity and the dynamics of frontal systems. Upwelling areas and frontal systems are regions of high environmental variability associated with decreased sizes with respect to the temperature-size trend.

In the Quaternary, environmental control of size change in planktic foraminiferal species has been documented in the Pleistocene (Bé and Duplessy, 1976; Malmgren and Kennett, 1978; Naidu and Malmgren, 1995). The size response to temporal environmental changes during glacial-interglacial cycles mimics the spatial Holocene size variations. The same processes, which drive geographic assemblage size changes in the Holocene, are correlated with short term temporal size variations in the Quaternary. The amplitude of assemblage size variation is directly related to the amplitude of the Quaternary climatic fluctuations (Chapter 4). More stable environments display the least assemblage-size variation. Assemblage-size variation may either be the result of species replacement or intraspecific size variation, or both. The relative importance of these processes depends on the environmental setting. In the subtropics and tropics, small temperature variations cause strong changes in the composition of the largest species in the assemblage since the temperature optima of the species are very close to each other. In the subpolar environment, the temperature optima of individual species differ greatly and the species have a wider temperature tolerance. Therefore, intraspecific size changes without species replacement are more likely to happen in this environment. During the Quaternary, species distributions and sizes oscillated along a north-south gradient. This implies that species are adapted to certain environmental conditions and persist as long as a suitable habitat can be found and occupied.

On longer time scales, evolutionary size changes become important. Results from previous studies suggest that climatic change is the principal instigator of evolutionary change within planktonic foraminiferal faunas in the Cenozoic (e.g. Ciffeli, 1969; Lipps 1970), and more specifically, that there is a fundamental linkage between amplitude of changes and steepness of surface water gradients and periods of speciation or extinction.

The size record in the Cenozoic can be divided into three different intervals, a time of dwarfs from the K/T boundary up to the late Eocene, a transition period from the late Eocene to the Mid-Miocene and a time of giants from the Mid-Miocene to Recent (Chapter 5). The early Paleogene is characterised by an increase in size ranges after the K/T reduction and similar foraminiferal assemblage size is at all latitudes, indicating little provincialism. In the middle Eocene, high latitude and low latitude assemblage sizes became decoupled as a consequence of the steepening of the latitudinal temperature gradients caused by cooling in the high latitudes (Lear et al., 2000). In the early Miocene, subtropical and tropical assemblage size become differentiated. A pronounced size increase in the Neogene is observable in all warm water sites studied, whereas high-latitude records display size stability during this period.

The large sizes of warm water late Neogene planktic foraminiferal assemblages are unprecedented in the geological record. This suggests that this increase in size is a reaction to niches partitioning as a consequence of the intensification of vertical and latitudinal temperature gradients. Size changes in the assemblage reflect a stronger stratification of the upper water column rather than temperature per se. Stratification results in an increase in the number of ecological niches, which allows for specific adaptations within the planktic foraminifers, including growth to large size. The similarity of size evolution of globorotaliid and globigerinid species (*G. menardii*, G. *sacculifer*, G. *ruber,* O. *universa*) argues against a lineage-specific explanation for large size.

At times of low species richness, such as the Paleocene and the Oligocene, the paleo-productivity of the surface oceans rather than the temperature structure seems more closely correlated to planktic foraminiferal size. This suggests a dependency of foraminifers on fertility and the importance of fertility after the breakdown in food chains following the K/T mass extinction (d'Hondt, 1998), and during the dominance of a "global upwelling" fauna proposed for the Oligocene (Hallock, 1987).

ZUSAMMENFASSUNG

Im Mittelpunkt dieser Arbeit stehen planktische Foraminiferen, eine bedeutende marine Mikrofossilgruppe, deren kalkreiche Schalen in großer Anzahl in marinen Sedimenten vorkommen. Anhand der einzigartigen Sedimente der Ozeane wurden die makroevolutive Veränderungen der Größenverteilung in Vergesellschaftungen planktischer Foraminiferen, der Einfluß physikalischer Faktoren auf morphologische Diversität, sowie biologische Reaktionen auf Störungen in der Umwelt untersucht. Internationale Bohrkampagnen (ODP, DSDP) ermöglichten die Untersuchung ungewöhnlich vollständigen, gut datierten Sedimentkernen aus den meisten Meeresregionen.

Kapitel 1 beinhaltet einen Überblick über frühere Arbeiten zur Größenentwicklung planktischer Foraminiferen. Diese haben gezeigt, daß die Gehäusegröße planktischer Foraminiferenarten in Beziehung zu Umweltbedingungen wie Temperatur (Bé et al. 1973; Hecht 1976), Fertilität (Naidu und Malmgren 1995) und der Variabilität der Umwelt (Bé und Duplessy, 1976; Naidu und Malmgren, 1995) steht. Evolutive Veränderungen der Gehäusegröße wurden ebenfalls bereits dokumentiert (Malmgren et al., 1983; Corfield und Shackleton, 1988; Kucera und Malmgren, 1998). Die meisten bisherigen Studien über evolutive Größenveränderung planktischer Foraminiferen basieren auf Analysen einzelner Arten oder phylogenetischer Abstammungsreihen (z. B. Malmgren und Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato und Thierstein, 1997; Kucera und Malmgren, 1998; MacLeod et al., 2000).

Die vorliegende Arbeit erweitert in den folgenden Kapiteln das Blickfeld von der Entwicklung der Größen einzelner Arten zur Größenveränderungen der gesamten Foraminiferen-Vergesellschaftung. Dadurch bietet sich die Möglichkeit, Einblicke in makroevolutionäre Prozesse über große Zeiträume zu gewinnen. Zu diesem Zweck wurden mit Hilfe eines automatisierten Lichtmikroskopes der maximale Durchmesser von mehr als 1,6 Millionen Foraminiferen in drei verschieden Datensätzen vermessen (Kapitel 2). So wurde zur Charakterisierung der Größenveränderung das Größenspektrum ganzer Foraminiferen-Vergesellschaftungen vermessen. Es zeigt sich, daß Größenspektren in Vergesellschaftungen in Richtung großer Individuen verzerrt sind. Daher wurde der Wert, der die größten 5% aller Individuen in einer Vergesellschaftung von den kleineren 95% trennt, als Schätzwert für die Größenveränderung verwendet.

Auf dieser methodischen Grundlage wurden drei verschiede Zeitintervalle behandelt. Zunächst wurde die Bedeutung ökologischer Einflüsse auf die Größenverteilung innerhalb von Foraminiferen-Vergesellschaftungen im Holozän untersucht und daran anschließend die Gültigkeit der aufgestellten Hypothesen im Spätquartär getestet und bestätigt. Danach wurden die neu gewonnen Erkenntnisse auf das gesamte Känozoikum übertragen, um die

Größenveränderungen in planktischen Foraminiferen-Vergesellschaftungen zu interpretieren.

Kapitel 3 zeigt, dass die geographische Größenverteilung innerhalb der planktischen Foraminiferen-Vergesellschaftungen im Holozän von Umweltgradienten abhängig ist, im besonderen von Temperatur und Fertilität des Ozeans (Kapitel 3). Als Hauptsteuerungsfaktoren wurden dabei Parameter identifiziert, die mit der Temperatur in Beziehung stehen. Die Größe innerhalb von Foraminiferen-Vergesellschaftungen steigt somit im Holozän von den Polargebieten zu den Tropen hin an. Allerdings ist dieser Anstieg nicht linear, sondern Sekundärparameter wie Fertilität oder die Dynamik von Frontensystemen verursachen Abweichungen. Stark schwankende Umweltbedingungen in Auftriebsgebieten und Frontensystemen behindern das Wachstum von Foraminiferen so stark, dass keine großen Individuen wachsen.

Es wurde bereits mehrfach dokumentiert, dass sich die Größen planktischer Foraminiferen Arten während des Quartärs durch zeitliche Variationen der Umweltbedingungen stark verändert (Bé und Duplessy, 1976; Malmgren und Kennett, 1978; Naidu und Malmgren, 1995). Die Reaktion von Foraminiferen auf zeitliche Veränderungen der Umweltbedingungen während glazial-interglazial Wechseln imitierend die vorher beschriebenen Holozänen Größenvariationen. Die gleichen Prozesse, wie Kapitel 4 demonstriert, welche geographische Veränderungen in der Größenverteilung in Vergesellschaftungen im Holozän beeinflussen, sind verantwortlich für hochfrequente zeitliche Veränderungen im Quartär. Die Amplitude der Größenveränderungen in den Vergesellschaftungen steht hierbei in direkter Beziehung zur Amplitude der quartären Klimaschwankungen (Kapitel 4). Stabile Ökosysteme weisen dabei die geringsten Größenveränderungen auf. Wie die Untersuchung dreier Kerne zeigte, können Größenveränderungen einzelner Individuen einer Vergesellschaftung das Ergebnis zweier Prozesse sein: Zum einem des Austausches von Arten und zum andern der Größenveränderungen innerhalb einzelner Arten. Die relative Bedeutung dieser Prozesse hängt von den Umweltbedingungen ab. In den Subtropen und Tropen rufen kleine Temperaturvariationen großen Veränderungen in der Zusammensetzung der Vergesellschaftungen hervor, da die Temperaturoptima einzelner Arten lediglich durch kleine Temperaturunterschiede voneinander getrennt sind. In subpolaren Gebieten liegen die Temperaturoptima der dort vorkommenden Arten weiter auseinander, und die Arten haben breitere Temperaturtoleranzen. Daher dominiert in diesen Ökosystemen die intra-spezifische Größenveränderung ohne den Austausch von Arten. Während der quartären Klimaschwankungen oszilliert die Verteilung von Arten und Größen entlang eines Nord-Süd Gradienten. Dieser Prozeß deutet an, dass die Foraminiferengrößen eine Adaption an bestimmte Umweltbedingungen widerspiegelt, die so lange erhalten werden kann, wie ein geeigneter Lebensraum gefunden und besetzt wird.

Über lange Zeiträume, wie z. B. das gesamte Känozoikum, werden evolutive

Größenveränderungen bedeutend. Die Ergebnisse früherer Arbeiten legen nahe, daß Klimawandel ein entscheidender Antrieb für evolutionäre Veränderungen in der Zusammensetzung von Faunen planktischer Foraminiferen ist (z. B. Cifelli, 1969; Lipps, 1970). Präziser ausgedrückt bedeutet es, dass es eine grundlegende Verbindung zwischen der Amplitude der Veränderung und der Steilheit des Oberflächenwasser-Gradienten mit Perioden der Bildung und des Aussterbens von Arten gibt.

Der Größendatensatz känozoischer Foraminiferen-Vergesellschaftungen kann in drei Intervalle eingeteilt werden: eine Zeit der Zwerge von der Kreide/Tertiär-Grenze bis ins späte Eozän, eine Übergangsphase vom späten Eozän zum mittleren Miozän und eine Zeit der Riesen vom mittleren Miozän bis heute (Kapitel 5). Im frühen Paläogen waren die Größen in Foraminiferen-Vergesellschaftungen in allen Breitengraden sehr ähnlich, was auf einen geringen Provinzialismus hindeutet. An der Grenze des mittleren zum späten Eozän entkoppelten die Vergesellschaftungen hoher und niedriger Breiten, was durch den Anstieg der latitudinalen Temperatur Gradienten, verursacht durch die Abkühlung in den hohen Breiten, resultiert (Lear et al., 2000). Im frühen Miozän entwickelte sich ein Unterschied zwischen Subtropen und Tropen. Ein deutlicher Größenanstieg im Neogen ist in allen Proben aus warmen Ozeanbereichen erkennbar. Im Gegensatz dazu zeigen Faunen aus hohen Breiten eine Größenstabilität während der gleichen Zeit.

Die außergewöhnliche Größe tropischer Foraminiferen-Vergesellschaftungen des Pliozäns und Pleistozäns ist beispiellos in den letzten 70 Millionen Jahren. Der Größenanstieg der Foraminiferen-Vergesellschaftungen kann als Beispiel für die Reaktion auf eine Intensivierung der vertikalen und latitudinalen Temperaturgradienten betrachtet werden. Größenveränderungen in den Vergesellschaftungen spiegeln hierbei die Stratifizierung der oberen Wassersäule wider und sind nicht direkt von der Temperatur abhängig. Eine stärkere Stratifizierung führt zu einer Zunahme der Anzahl ökologischer Nischen, so dass spezifische Adaptionen planktischer Foraminiferen möglich sind, wie z. B. das Wachstum zu größeren Individuen. Die Vergleichbarkeit des Grössenwachstums globorotaliider und glogiberinider Arten (*G. menardii*, G. *sacculifer*, G. *ruber,* O. *universa*) spricht gegen eine ausschliesslich von der Evolutionsreihe abhängigen Erklärung.

In Zeiten allerdings, in denen die Vergesellschaftungen nur aus wenigen Arten bestehen, wie dem Paläozän und dem Oligozän, ist die Produktivität im Oberflächenwassers für die Größenveränderungen planktischer Foraminiferen entscheidender als die Temperatur. Dieses Ergebnis unterstützt die Annahme, dass Foraminiferen von der vorhandenen Nahrung abhängig sind, und dass nach dem Zusammenbruch der Nahrungskette nach dem Massenausserben an der Kreide/Tertiär-Grenze (d'Hondt, 1998) und während der Dominanz der Oligozänen „globalen Auftriebsvergesellschaftung" (Hallock, 1987) die Fertilität eine große Bedeutung hat.

RÉSUMÉ

Les foraminifères planctoniques sont un groupe important de microfossiles calcaires, leur test étant abondant dans la plupart des sédiments océaniques. Le registre fossile pélagique est exceptionnellement complet, avec une couverture globale grâce à un ensemble de carottes bien datées provenant des programmes de forage internationaux (DSDP, ODP).

Grâce à ce registre fossile d'une qualité exceptionnelle, les changements macro-évolutifs de taille des assemblages de foraminifères planctoniques ont été analysés. Les variations de taille des assemblages ont été envisagées en tant que conséquence de l'impact des facteurs physiques sur la diversité morphologique, ou comme réponse biotique à des perturbations environnementales. Des travaux antérieurs ont montré que la taille du test des espèces de foraminifères planctoniques varie en fonction de paramètres écologiques tels que la température (Bé et al. 1973; Hecht 1976), l'intensité d'un upwelling (Naidu and Malmgren 1995), ou la variabilité environnementale (Bé and Duplessy, 1976; Naidu and Malmgren, 1995). De plus, la taille du test a connu des variations au cours de l'évolution (Malmgren et al., 1983; Corfield and Shackleton, 1988; Kucera and Malmgren, 1998) (Chapitre 1). Cependant, la plupart des études considérant les variations évolutives de taille étaient jusqu'à présent centrées sur une espèce ou une lignée (Px. Malmgren et Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato et Thierstein, 1997; Kucera et Malmgren, 1998; MacLeod et al., 2000).

La présente thèse propose d'étendre l'étude des variations de taille d'une seule espèce à l'assemblage entier des foraminifères planctoniques. Cette approche présente l'intérêt de pouvoir s'intéresser aux tendances et processus macro-évolutifs à long terme. Dans ce but, le diamètre maximum de plus de 1,6 millions de foraminifères, répartis en trois corps de données, a été mesuré par un microscope optique automatisé (Chapitre 2). Le spectre des tailles montrant une distribution exponentielle, la valeur définissant la séparation entre le 5% des individus les plus grands du 95% des microfossiles les plus petits est considérée comme une estimation de variation de taille. Dans un premier temps, les influences écologiques possibles sur la taille des assemblages ont été identifiées sur un ensemble d'échantillons holocènes. La validité des résultats obtenus a ensuite été testée et confirmée dans le Quaternaire récent. Les conclusions de ces études ont finalement servi de base à l'interprétation des variations de taille des assemblages de foraminifères planctoniques au long de tout le Cénozoïque.

D'un point de vue géographique durant l'Holocène, la taille des assemblages de foraminifères dépend des gradients environnementaux dans l'océan, notamment de température et de productivité primaire (Chapitre 3). Les effets liés à la température apparaissent comme le facteur principal influençant les variations de taille, impliquant une augmentation de taille depuis les régions polaires jusqu'aux zones biogéographiques tropicales. Cependant, cet accroissement de taille n'est pas régulier, et des déviations sont observées, interprétées comme étant la conséquence de facteurs environnementaux secondaires, à savoir la productivité primaire et la dynamique des systèmes frontaux. Les zones d'upwelling et de systèmes frontaux sont en effet caractérisées par une forte variabilité environnementale diminuant la taille des assemblages, en comparaison avec la taille attendue à partir de la relation observée avec la température.

Ce contrôle environnementale de la taille des espèces de foraminifères planctoniques avait été documenté auparavant concernant le Quaternaire (Bé and Duplessy, 1976; Malmgren and Kennett, 1978; Naidu and Malmgren, 1995). D'une manière générale, au cours du Quaternaire récent, la réponse de la taille aux variations environnementales caractérisant les cycles glaciaires-interglaciaires suit les mêmes schémas que les variations spatiales observées durant l'Holocène. La présente étude montre que l'amplitude des variations de taille dans les assemblages est également directement proportionnelle à l'amplitude des fluctuations climatiques quaternaires (Chapitre 4), les environnements stables montrant le moins de variabilité de taille. Les variations de taille des assemblages peuvent être le résultat du remplacement d'espèces, ou des variations intraspécifiques de taille. L'importance relative de ces deux processus dépend de la situation environnementale. Dans les zones subtropicales et tropicales, de faibles variations de température causent d'importants changements dans la composition des plus grandes espèces de l'assemblage, car les différentes espèces ont des optimums écologiques proches les uns des autres. Dans les environnements subpolaires, les espèces ont une plus grande tolérance à la température; les optimums des différentes espèces sont donc répartis de manière plus lâche en fonction des gradients environnementaux. En conséquence, les variations de taille intraspécifiques, sans remplacement d'espèces, sont plus probables dans cet environnement. Durant le Quaternaire, la distribution des espèces et le gradient de taille a oscillé selon une direction nord-sud. Ce résultat montre que la taille d'une espèce est liée à son adaptation à un contexte écologique donné, adaptation qui persiste sans modification majeure tant qu'un habitat favorable correspondant est disponible.

A plus grande échelle temporelle, comme par exemple pour le Cénozoïque, les modifications de taille dues à des processus évolutifs deviennent importants. Des travaux antérieurs suggèrent que les variations climatiques seraient la cause principale des changements évolutifs pour les faunes de foraminifères planctoniques (Cifelli, 1969; Lipps 1970). L'hypothèse d'un lien entre l'amplitude des changements climatiques et des clines dans les eaux de surface d'une part, et des périodes de spéciation ou d'extinction d'autre part, a ainsi été avancée.

Le registre du Cénozoïque peut être divisé en trois intervalles, en ce qui concerne la taille des assemblages. De la limite Crétacé / Tertiaire à l'Eocène tardif, les assemblages sont essentiellement composés de petits individus, expression d'un nanisme post-crise. De l'Eocène tardif au Miocène moyen, se situe une période de transition conduisant à un intervalle caractérisé par le gigantisme de certains spécimens, du Miocène moyen au Récent (Chapitre 5).

Durant le début du Paléogène, la taille des assemblage est similaire à toutes les latitudes, indiquant un faible provincialisme. Au cours de l'Eocène moyen, la taille des assemblages de hautes et basses latitudes diverge, conséquence de l'accentuation des gradients latitudinaux de température couplée au refroidissement des hautes latitudes (Lear et al., 2000). Au début du Miocène, les assemblages subtropicaux et tropicaux voient également leur taille se différencier. Un accroissement de taille durant le Néogène s'observe dans toutes les régions tropicales et subtropicales étudiées, tandis que les sites de hautes latitudes montrent une stabilité de la taille des assemblages.

Les grandes tailles observées dans les assemblages des foraminifères planctoniques de basse latitude au cours du Néogène supérieur sont sans précédent dans le registre fossile. Cette augmentation de taille pourrait être une réponse à l'intensification des gradients de température verticaux et latitudinaux. Cependant, les changements de la taille des assemblages ne sont pas directement dépendants de la température, mais refléteraient plutôt une stratification plus marquée de la tranche d'eau supérieure. De cette stratification résulterait une augmentation des niches écologiques possibles, permettant des adaptations fines favorisant la croissance des foraminifères planctoniques jusqu'à des tailles plus grandes.

Durant les intervalles caractérisés par des niveaux de diversité spécifique plus réduits, tels que le Paléocène et l'Oligocène, la taille des assemblages de foraminifères planctoniques semble davantage dépendante de la fertilité des eaux de surface que de la température. Ces hypothèses démontrent la dépendance des foraminifères de la productivité après le collapse de la chaîne alimentaire qui a suivi l’extinction de masse de la limite Crétacé-Tertiaire, ainsi que l’idée d’un assemblage faunistique “d’upwelling global” proposé pour l’Oligocène (Hallock, 1987).

CHAPTER 1

INTRODUCTION

The goal of this thesis is to quantify and to understand the ecological, paleobiogeographical and evolutionary significance of size variability in planktic foraminiferal tests during the Cenozoic.

1.1 THE INVESTIGATED GROUP: PLANKTIC FORAMINIFERS

Planktic foraminifers are a major marine calcareous microfossil group. They are small (up to 1500 µm), grow by adding chambers and have a relatively simple “bauplan” (Berger, 1969) that is well documented over geologic time (Cifelli, 1969; Norris, 1991).

Due to their great abundance and their good fossilisation potential, foraminifers are used for biostratigraphic, paleoceanographic, and paleobiogeographic studies (see Hemleben et al., 1989 and references therein). Because of their great utility, much has been learned about their stratigraphic ranges and paleogeographic distribution of planktic foraminiferal species. The phylogenetic relationships are known for the most abundant and many minor species (Kennett and Srinivasan, 1983; Bolli et al., 1985). The most common application of foraminifers is for biostratigraphic dating and investigations of paleoceanographic changes. Paleoceanographic interpretations are based on changing species composition, shell chemistry (see references in Fischer and Wefer, 1999) or morphological change of single species. Morphological criteria used in such studies include size, shape and coiling properties of the test (e.g. Ericson, 1959; Bé et al., 1973; Hecht, 1976; Naidu and Malmgren, 1995; Naidu and Malmgren, 1996).

In the marine environment, size change in microorganisms is used to assess water-mass conditions, temperature and primary productivity. Recent studies have focused on oxygen availability as the factor controlling size in amphipods (Chapelle and Peck, 1999), benthic foraminifers (Kaiho, 1998), and gastropods (McClain and Rex, 2001). The size of planktic foraminifers is influenced by the physico-chemical properties such as temperature, salinity, carbonate saturation, and nutrient and oxygen availability of the surrounding environments (e.g. Berger, 1969; Bé and Tolderlund, 1971; Caron et al., 1981; Caron et al., 1987; Bijma et al., 1992; Schiebel et al., 2001).

Since their origin in the mid-Jurassic, planktic foraminifers, as a group, have undergone at least three periods of diversification (Loeblich and Tappan, 1985), each of which is thought to have involved a general increase in test size (Norris, 1991; Arnold et al., 1995). An iterative evolution has been documented (Cifelli, 1969; Cifelli and Scott, 1986; Norris, 1991) with "primitive globigerinid" forms of generally small size dominating the assemblage after the K/T-boundary, which subsequently developed into a highly diverse assemblage (Bolli et al., 1985). Low diversity faunas, described as "oligotaxic fauna" (Kennett, 1982), again dominated in the Oligocene, giving rise to a diverse Miocene assemblage.

Thus their long paleontological history and their high abundance and global occurrence in marine sediments make planktic foraminifers extremely well suited for examining the influence of ecology and evolution on size variation in the marine environment.

1.2 THE IMPORTANCE OF BODY SIZE

The study of large-scale evolutionary patterns has been the domain of paleontology for two centuries. The origin of major innovations and the underlying causes for the radiation of form, that is size and shape, is one of the most challenging questions in biology (Caroll, 2001). Key questions include: (1) which biotic and physical factors affect biodiversity, (2) what is the ecological basis for non-random introduction of evolutionary innovations in time and space, and (3) what are the patterns of biotic response to environmental perturbations and the dynamic feedback between life and the Earth's surface processes (Jablonski, 2000)? Specifically, the physical boundary conditions controlling rates, magnitudes, spatial scale and frequency of biotic change are still poorly understood (Jablonski, 2000). It is still not clear why some phylogenetic lineages flourish while others fail; why some epochs are denoted by major radiation and others by extinction; and why some environments support diverse fauna and others impoverished faunas (Reaka and Manning, 1987). The relative importance of biotic or physical factors in initiating speciations and extinctions in the history of life is still uncertain, and a subject of much controversy. unterstood.

Recently, there has been an increased interest in the factors controlling size (Peters, 1983; Calder, 1984; Reiss, 1989; Brown, 1995 and references therein). Size is an obvious morphological characteristic, readily preserved in fossils, easy to measure, conspicuous, ecologically important, comparable across taxa and extremely variable through time and space. Consequently, this parameter has been studied for several groups of organisms (Peters, 1983; Skelton, 1993; Futuyma, 1998).

Several important processes linked to the ecology of an organism depend on size (volume or surface area). Among these are metabolism, respiration, ingestion and a number of related phenomena, including predator-prey relations, resistance to starvation and aspects of life history (Peters, 1983). Some processes depend on the surface area, others on volume. Size changes affects these two parameters in different ways: isometric features increase with the cube of linear dimensions, while surface-area related features increase only with the square of linear dimensions. Thus, surface-area-dependent processes, such as feeding, respiration, and skeletal support, have to keep pace with volume and weight increases.

Size change occurs in response to selection pressure resulting from one or more advantages. Proposed advantages of large size are improved ability to capture prey or avoid predators, greater reproductive success, expanded size range of acceptable food, decreased mortality, extended individual longevity and increased heat retention per unit volume (Stanley, 1973). Yet, large size also has disadvantages. For instance, feeding efficiency must increase substantially. Shelled organisms require a disproportionately large development in shell thickness to match an increase in the body volume. In addition, planktic organisms must compensate for their greater weight to maintain buoyancy.

Changes in size can be attributed to different processes. The size of a single specimen is constrained by its genome, ontogeny and environment (Seilacher 1992). The environment has an important influence on the size of organisms at the species level. For example, Bergman's rule states that body-size increases towards high latitudes in terrestrial mammals whereas Allen's rule states that the appendages get shorter in the same group. Both rules aim correlated the decrease in relative size of exposed portions of the body with respect to its volume with decreasing temperature. A reduced body surface diminishes gas exchange and heat loss, two processes which are very important in water. This is an example of ecophenotypic variability in morphology. Speciation (according to Cope’s rule an increase in body-size along a lineage) also influences body size (phyletic size change). Modern distributions are a snapshot of the evolutionary size trends. Change in size and the mechanism related to these changes over evolutionary time scales will be discussed in more detail.

1.3 MACROEVOLUTION AND MACROECOLOGY

Changes in size can be considered at different taxonomic levels. The factors that determine the shape of large-scale size trends have to be investigated with 'macroscopic' approaches. Such approaches sacrifice the detail of local-scale studies in the hope of identifying general principles or broad patterns in evolutionary and ecological systems and are known as “Macroevolution” and “Macroecology” (Brown, 1995; Caroll 2001). Macroevolution is the investigation of the evolutionary change above the species level and the processes leading to the formation of new species. Macroecology tries to elucidate ecological processes influencing higher order taxonomic groups on a global scale.

A study of the macroecology and macroevolution of foraminifers must incorporate information from a wide range of latitudes and oceans over long time-scales. Different evolutionary radiations have occurred in both temperate and tropical regions. Some lineages began in temperate areas and later shifted to the tropics. Consequently, size changes ought to be studied in globally-distributed populations or assemblages.

Most studies of evolutionary size changes in planktic foraminifers have focused on single species or lineages (e.g. Malmgren and Kennett, 1981; Arnold, 1983; Malmgren et al., 1983; Spencer-Cervato and Thierstein, 1997; Kucera and Malmgren, 1998; MacLeod et al., 2000). Such studies on single species have provided regional ecological and stratigraphic information on size change. Studying entire planktic foraminiferal assemblages, in addition to single species, has the potential to provide insight into long-term macroevolutionary processes or global environmental changes.

Phyletic size increase, first formulated as Cope’s rule, is assumed to be a widespread trend in paleobiology (Arnold et al., 1995). Size trends can be active (biased replacement) or passive (increase in variance within a clade or group, Gould 1988). Traditionally, evolutionists interpret trends as evidence for natural selection (Wagner, 1996). Alternatively, evolutionary trends might be driven by differential speciation and/or survivorship of entire species based on morphological characters (Stanley, 1975; McShea, 1994).

Size increase is more common than size decrease, since adaptive breakthroughs leading to new taxa tend to arise at relatively small body size and extinction often occurs in large, structurally specialised lineages (Stanley, 1973). Specialisation appears to be correlated with size. Unspecialized species, having simple structures, are commonly small, whereas nearly all large taxa are specialised. The adaptive barrier seems lower at small size. If a radiation starts near a boundary condition for a group, the tendency will be to expand away from it (Gould, 1988; Norris, 1991; Arnold et al., 1995). Niches for larger body size tend to be filled subsequently.

Hence, the expansion of morphological variance over time (Stanley, 1973; Norris, 1991; McShea, 1994) can be related to the fact that the evolution often starts near some “limiting boundary” also termed the “left wall”. Limiting boundaries in body size (Stanley, 1973) can occur in aspects of shell construction (Norris, 1991) and morphological complexity (McShea, 1994). Therefore, Cope’s rule can be interpreted as an evolutionary trend away from small size rather than toward larger size (Stanley, 1973). The tendency toward larger size within a taxon produces an increase in mean and maximum size, but not necessarily in minimum size (Bonner, 1968; Gould, 1988). Stanley (1973) states that the disadvantages rather than the advantages of size increase limit evolutionary innovations to small sizes.

Size changes through time can be attributed either to adaptation or speciation. Within some lineages, the original niche will remain unchanged during evolution. Size change will simply improve adaptation to the environment. On the other hand during major diversification events, numerous lineages will change body sizes, with or without major niche transitions (Stanley, 1973). The mean overall size trend depends on the position of the ancestor of the higher taxon within the size-frequency distribution of the higher taxon. Stanley (1973) assumes that pronounced size change are associated primarily with speciation events, although trends of gradual intraspecific body size increase is not ruled out.

1.4 THE RATE OF CHANGE IN THE FOSSIL RECORD

Since the evolution of a taxon often influences its morphological characteristics, the speed of evolutionary and hence morphological change is a critical point in this analysis. The question whether evolutionary change is gradual or abrupt (punctuated) within lineages has generated much discussion. Gradual transformations of entire populations into new species have been documented in free-living marine plankton (Malmgren and Kennett, 1981; Arnold, 1983). This process, phyletic gradualism, can be seen as gradual morphological change through time in lineages. Phyletic gradualism assumes that lineages evolve without a general tendency for evolutionary acceleration during speciation events. Gradual change has been explained by the lack of geographical barriers in the open-ocean environment (Sheldon, 1990; Sheldon, 1996).

In contrast, punctuated equilibrium describes rare but rapid bursts of morphological change, interrupting stasis in fossil lineages (Eldredge and Gould, 1972). This results in the splitting of lineages (cladogenesis). The process behind punctuated equilibrium is assumed to reflect allopatric isolation of a small part of the entire population. Hence, large populations should be in stasis or morphological equilibrium. Morphological change accompanying the speciation of these peripherally isolated populations would be accomplished in a relatively short period of geologic time. The transition period should be shorter than 1% of the total duration of the descendant species to be termed “punctuated” (Gould, 1982).

A mixture between both processes is termed punctuated gradualism (Malmgren et al., 1983). Punctuated gradualism involves anagenetic speciation at lower rates than postulated for the punctuated equilibrium. Anagenesis is defined as speciation with modifications within a single lineage or an established species. In contrast to the phyletic gradualism, punctuated gradualism involves cladogenesis.

1.5 THE MECHANISM OF CHANGE

Evolutionary change requires mechanisms. Change in the developmental rate of an organism, heterochrony, provides a set of growth strategies that can cause significant morphological change between parent and daughter populations (Brenchley and Harper, 1998). New morphologies can be generated by altering the relationships between size, shape and time. Since structural complexity limits evolutionary potential, large and complex taxa are poorly suited for playing major ancestral roles (Stanley, 1973).

Sudden and profound reductions in both size and specialisation do not easily occur and have mostly been associated with mass extinctions. Additionally, an evolutionary mechanism in which one or more juvenile characters is transferred to the adult stage (e.g. the juvenile form becomes a sexually mature adult) is likely to produce major evolutionary transitions at small size (Stanley, 1973). Heterochrony is defined as a change in the timing or rate of developmental events, relative to the same events in the ancestor. Consequently, heterochrony is assumed to be the driving force for evolutionary change, producing important adaptive breakthroughs at relatively small body size. Changes in the timing of developmental events can be caused either by overdevelopment (peramorphosis) or underdevelopment (paedomorphosis). Peramorphosis results from acceleration (faster development), predisplacement (earlier onset of a development) or hypermorphosis (later offset of development). Paedomorphosis results from neoteny (slower development), postdisplacement (later onset of development) or progenesis (earlier offset of development). Peramorphosis is recognised by an increased rate of shape change or an extension of its period of operation, whereas paedomorphosis is observed as a reduced rate of change or a contracted period of operation.

1.6 THE CENOZOIC ENVIRONMENT: WHAT PERTURBATIONS DO WE EXPECT?

Environmental stress can push biota beyond their limits of adaptation. Speciation accompanied by morphological change, and ecophenotypic size variability can both result from environmental change. In general, the marine fossil record documents relative evolutionary stability in well-established species occupying ecosystems with low barriers compared with the terrestrial ecosystems. Central populations of these species are believed to exhibit greater evolutionary stability than isolated peripheral populations (Stanley, 1973). Marine planktic organisms are generally very broadly distributed, covering large areas of the ocean. Distributions and structure of planktic assemblages is dictated by ocean water masses. Distributions generally are confined by major oceanographic features, which changed during the Cenozoic.

The Maastrichtian was a time of high global temperature and a low thermal gradient between the poles and the tropics when compared with the present. The end of the Maastrichtian (K/T boundary) is defined by a mass extinction, which dramatically affected planktic foraminifers (MacLeod, 1995). Afterwards, the diversity of foraminifers was extremely reduced (Tourmarkine and Luterbacher, 1985). The biogenic carbon flux from the surface ocean to the deep sea collapsed and did not recover for at least 3 Myrs (d' Hondt et al., 1998). Depleted $\delta^{13}C$ values and minimal vertical $\delta^{13}C$ gradients compared with the Late Maastrichtian and the mid-Paleocene are assumed to be a consequence of ecosystem reorganisation due to the absence of large grazers or decrease in the size of phytoplankton. This reduction of the export production finally recovered around 61 Ma. During the Danian, the planktic foraminiferal diversity started to recover to previous values (Tourmarkine and Luterbacher, 1985). An abrupt episode of global warming, known as the Late Paleocene Thermal Maximum (LPTM) marked the end of the Paleocene epoch (Kennett and Stott, 1991). This prominent event is characterised by a 5-6°C rise in bottom waters (Kennett and Stott, 1991) and 8°C rise in high-latitude surface temperatures. Carbon isotope data suggest that degassing of biogenic methane hydrate may have been an important factor in altering the Earth's climate (Dickens et al. 1995). The LPTM has been related to a mass extinction of benthic foraminifers and a widespread proliferation of exotic planktic foraminiferal taxa (Kelly et al., 1996).

Around 50 Ma, a gradual cooling began (Zachos et al., 1994; Zachos et al., 2001; Lear et al., 2000), leading to sea ice production, glaciation on Antarctic and cooling of surface and bottom waters at the end of the Eocene (Shackleton and Kennett, 1975). The middle/late Eocene faunal boundary event is marked by the expansion of cool-water assemblages, following a major extinction event among warmer-water species involving 80% of the individuals or 23% of the foraminiferal species (Keller et al., 1987). This event is connected with the onset of, at least shallow, Circum-Antarctic circulation (Kennett and Watkins, 1976). In the late Eocene, the warm water subtropical gyre decoupled from the colder, subantarctic gyre, initiating a subtropical front (Kennett, 1978).

In the Oligocene, deepening of the Drake Passage (Barker and Burrell, 1977) caused a reduction of the meridional heat flow and a steepening of latitudinal temperature gradients. The change in circulation led to increased zonal winds and thermocline evolution (Vincent and Berger, 1985). The thermal isolation of Antarctica led to an extensive build up of ice sheets. Faunal changes, however, were less dramatic than in the mid-Eocene. Just four species became extinct at the Eocene-Oligocene boundary (Corliss et al., 1984). The complete extinction of typical Eocene fauna, which began at the mid/late Eocene boundary, occurred during another major faunal turnover around the boundary of the early to late Oligocene (28.5 Ma) (Keller et al., 1987). Newly evolved Oligocene species were generally adapted to colder conditions with the lowest diversity since the K/T event (Kennett, 1982). This turnover happened abruptly at high latitudes and gradually in subtropical to tropical regions (Kennett, 1982). Since that time, foraminiferal assemblages at high latitudes have been similar to present ones.

Beginning in the late early Miocene, fine-grained diatomaceous, organic-rich sediments were deposited around the northern Pacific margins, an interval known as the “Monterey Event” lasting from 18 to 12.5 Ma (Vincent and Berger, 1985). These sediments were deposited as a result of intense upwelling, a consequence of the development of strong zonal winds and a strong permanent thermocline. Concurrent cooling strengthened the thermocline development (Vincent and Berger, 1985). In the mid-Miocene, a transient warming event temporarily interrupted the cooling process. The mid-Miocene Climatic Optimum, around 17 to 15 Ma (Zachos et al., 2001), was again followed by global cooling with the re-establishment of a major ice-sheet in East Antarctica by 10 Ma (Vincent et al., 1985). Additional cooling and ice-sheet expansion in West Antarctica (Kennett and Barker, 1990) is indicated by rising of $\delta^{18}0$ values into the early Pliocene.

The early Pliocene was characterised by a subtle warming trend, starting in the latest Miocene around 6 Ma, and lasting until 3.2 Ma (Pliocene Climate Optimum), followed by the onset of Northern Hemisphere glaciation, indicated by $\delta^{18}0$ values from benthic foraminifers (Shackleton et al., 1988). Around 4.5 Ma, the Panamanian seaway closed, leading to a change in provincialism and diversity of planktic biota. Since 2.5 Ma, pronounced cyclic changes in ice volume are found in the geological record, which lead to sea level fluctuations and a higher oceanic turnover rate.

1.7 THESIS OVERVIEW

The main focus of this thesis is to investigate the macroecological and macroevolutionary patterns of planktic foraminiferal assemblages and to determine possible causes for size changes during the Cenozoic. To investigate the importance of the extinction event at the K/T boundary on size of planktic foraminifers, some Maastrichtian samples are included in this study.

The goal of this thesis is to quantify and attempt to understand the paleoecological, paleobiogeographical and evolutionary significance of size variability in planktic foraminiferal tests. The modern geographic and ecological patterns of size variability will first be documented in a representative set of Holocene surface sediments. A set of initial hypotheses linking size with geographic and ecological variables will be tested in the Late Quaternary. Then, size variability in total planktic foraminiferal assemblages will be documented throughout the Cenozoic for the most important biogeographic areas. The hypotheses developed for the Holocene will be used to analyse the size patterns in the Cenozoic. This study will yield a large set of test measurements, showing both geographical and temporal patterns, likely controlled by various environmental and evolutionary processes. A new quantitative data set on repetitive evolutionary radiation of this group will test various hypotheses concerning evolutionary change in size.

1.7.1 Automated foraminifera size measurements using incident light microscopy (Chapter 2)

Most morphological studies of fossils are done manually, although manual collection of a statistically significant number of unbiased and reproducible data is time consuming. Large sample sets, covering the most important environmental gradients and long time scales, are necessary to disentangle the influence of ecology and evolution on size variability in microfossils. Only a few global or larger regional datasets are available (Hecht, 1976; Rex and Etter, 1998; Chapelle and Peck, 1999), despite the increasing focus on factors controlling size. To gather the necessary amount of size data, we built a robot that autonomously measures particles in the size range of planktic foraminifers under incident light. The robot captures about 1000 images of particles larger than 150 µm per hour and extracts several morphological features reliably, including diameter and area. This setup made the analysis of 784 samples possible, counting all together more than 1.6 million images.

1.7.2 Size distribution of Holocene planktic foraminifer assemblages: biogeography, ecology and adaptation (Chapter 3)

The Holocene investigation is a first step towards analysis of size changes of planktic foraminifers in the late Phanerozoic. In order to understand the ecological significance of size variability, I have analysed planktic foraminiferal assemblages of 69 Holocene samples, all together 114.991 measurements. The variation in test sizes of entire planktic foraminiferal assemblages results from numerous processes acting on at least three different spatial scales: On a global scale, size increase from the poles to the tropics can be attributed to the co-variation of several temperature-related effects, whereas on a regional scale primary productivity may become important. Intraspecific size variability also depends on physico-chemical and biotic constraints. The close correlation between maximum size and relative abundance of individual species with global temperature allows for the definition of environmental optima.

The size increase with increasing temperature is not monotonous. Rather it shows two local minima, one at 2°C the other around 17°C, where polar and subtropical fronts are found. These fronts represent major environmental perturbations and create unfavourable conditions, which result in a lower diversity and smaller sizes. Assemblages from upwelling areas also show smaller sizes due to species replacement and a decrease in size of the persisting symbiont-bearing species caused by turbidity (Ortiz et al., 1995).

1.7.3 Reaction of planktic foraminifers size to Late Quaternary climate change (Chapter 4)

The Quaternary is a period characterised by large environmental variations, related to the glacial-interglacial cycles. Within the literature both species size fluctuations and stability over time have been documented. Several studies have shown that, in the vicinity of frontal systems or in upwelling areas, species size fluctuates in the Quaternary (Bé and Duplessy, 1976). In contrast, some studies show no size variation (Malmgren and Healy-Williams, 1978), which can be interpreted as an indication of stable environmental conditions.

I have tested the variability of assemblage size changes over time and the validity of Holocene ecological relationships during the Quaternary temporal climatic fluctuations. I focused on the late Quaternary glacial-interglacial changes, since these climatic fluctuations are well constrained due to the numerous paleoceanographic proxies available. To cover an adequate biogeographic gradient, three cores from the South Atlantic were selected, corresponding to the subpolar, subtropical and equatorial upwelling zones. Size analyses in these cores revealed the following:

1. Test sizes in late Quaternary planktic foraminiferal assemblages depend on the same processes (temperature, primary productivity and frontal systems) as Holocene assemblages and these processes also drive temporal size variations.
2. The glacial-interglacial fluctuations display different amplitudes depending on geographic setting. The most stable environments display the least assemblage size variability. In variable environments, the processes involved in assemblage size change can be different, that is either species replacement or intraspecific size variations, or a combination of both. The balance between these effects reflects the geographic setting, especially the existing temperature range.
3. Species size depends on temperature. Each species has its optimum temperature. The optima for different species are clustered along the temperature gradient and are not equally distributed. The balance between species replacement and intraspecific size variation depends on the setting of the core regarding the distribution of optima of species. In the subtropics and tropics, a small temperature variation has a large impact of species replacement, since these optima are densely clustered. In the subpolar environment, species optima are less closely clustered and temperature tolerance of species is wider. Therefore, intraspecific size changes rather than species replacement are more likely to occur in subpolar environments.

The similarity between the results for the Holocene and Quaternary records suggests that the temperature optima of the investigated species did not change much during the last 300 kyrs. Therefore, the use of a modern analogue for paleoceanographic reconstructions based on planktic foraminifers is supported by our results. Expanding our approach to a longer record may help us recognise where the influence of evolutionary change becomes dominant.

1.7.4 The role of environmental change on size variation in planktic foraminiferal assemblages during the Cenozoic (Chapter 5)

Habitat tracking, a north-south oscillation in the distribution of Quaternary species with respect to temperature change, demonstrates the stability of species morphologies despite environmental change, as long as a suitable habitat can be found and occupied. Habitat tracking suggests that stabilising selection, rather than directional selection, will be the rule, as long as species can continue to “recognize” and occupy suitable habitat under a regime of environmental change (Eldredge et al., 1997). Hence, the question arises as to what amplitudes of environmental change are necessary to give rise to key innovations. The influence of extrinsic factors on size may be identifiable through the demonstration of repeated coincidence of morphological and evolutionary change with environmental changes inferred from independent paleo-proxies.

In general, the assemblage size pattern in the Cenozoic can be divided into three major phases: a time of dwarfs from the K/T boundary until ~42 Ma, a time of intermediate size from 42 to 14 Ma and a time of giants ~14 Ma until recent. In the early Paleogene, foraminiferal assemblage size shows a similar size range at all latitudes indicating little provincialism. In the mid-Eocene, high latitude and low latitude assemblage size became decoupled from each other, probably as a consequence of the steepening of the latitudinal temperature gradients due to high latitude cooling (Lear et al., 2000). In the early Miocene, subtropical and tropical assemblage size become differentiated. A pronounced Neogene (Mid-Miocene to recent) size increase is observed in all of the studied warm water sites, whereas at high-latitudes sizes remain rather constant during this period. The large sizes of Holocene planktic foraminiferal assemblages are unprecedented in the geological record.

Environmental change has been identified as a most important factor driving the size variations in the Cenozoic. Both temperature and productivity influence the size with time. In times of major reorganisation, as in early Paleogene or late Eocene to late-Oligocene, trophic relationships influence these low diversity faunas. As soon as diversity is regained, stratification in the upper water column and, consequently, the heterogeneity of available niches influence the necessity/ability to grow towards larger sizes. The close correlation of changes in stratification in the Neogene with the unprecedented size increase in low-latitudes suggests size evolution in planktic foraminifers is an active trend. I disfavour the possibility of a simple increase in variance as proposed by Jablonski (1997) and Stanley (1973) to explain the Cenozoic size record of planktic foraminifers, since there is no straightforward correlation with diversity. My data, however, do not allow statistical tests for this hypothesis. Increase in variance seems to be most important in low diversity "crisis" assemblages, such as the early Danian and the Oligocene.

The size trends observed are closely linked with climatic changes, suggesting that abiotic factors rather than random biotic interactions drive size. Consequently, the stationary model proposed by Stenseth and Maynard Smith (1984) seems to best explain size evolution. The model is not just applicable to the size data, as it also explains fluctuations in diversity, morphological complexity and changes in distribution (Lipps and Valentine, 1970).

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CHAPTER 2*

FULLY AUTOMATED GRANULOMETRY OF DEEP-SEA SEDIMENTS USING AN INCIDENT LIGHT MICROSCOPE

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ABSTRACT

Manual collection of a statistically significant quantity of unbiased and reproducible data on grain size and grain shape, e.g., of microfossil morphology, is time consuming. Therefore, there is a need to fully automated operating robots that recognise and analyse particles such as microfossils. Here, a robot is described that independently measures the size and shape of randomly oriented planktic foraminiferal tests using an incident light microscope. The robot is able to capture about 1000 images of grains larger than 63µm per hour and then extracts prominent morphological features including size. The system has been used to successfully complete about 400 deep-sea sediment analyses. The robot can also be used for automatic analysis of particles other than planktic foraminiferal tests because elementary problems such as contrast and focus on an incident light microscopes have been overcome using low reflectance and levelled glass trays.

2.1 INTRODUCTION

Automated particle analysis is a common application in biology (e.g., analysis of cell size and shape), quality control (e.g., wafer inspection systems) and in forensic sciences (e.g., detection of gunshot residues). In geoscience, particle analyses are widely done to characterize sediments (Felix 1969; Schwarcz and Shane 1969; Ehrlich and Weinberg 1970) or to quantify the morphology of fossils (Kennett 1968; Bé et al. 1973; Hecht 1976). However, there are only a few applications that take advantage of automated particle analysis (e.g., Ratmeyer and Wefer 1996; Young et al. 1996; Dollfus 1997; Bollmann et al. in press). Morphological studies of microfossils are usually done manually (Kennett 1968; Bé et al. 1973; Hecht 1976; Lazarus et al. 1995; Bollmann 1997; Knappertsbusch et al. 1997), despite the fact that the manual collection of a statistically significant amount of unbiased and reproducible data is time consuming. Therefore, size and shape analyses of microfossils are not routinely applied (e.g., for paleoceanographic reconstruction) although morphological variations of organisms have been shown to reflect past environmental and evolutionary changes (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Knappertsbusch et al. 1997; Bollmann et al. 1998; Rex and Etter 1998). The same holds true for planktic foraminifers, a keystone group within the marine ecosystem since the middle Jurassic (Bé et al. 1973; Hecht 1976; Arnold 1983; Lohmann & Malmgren 1983; Wei & Kennett 1988; Arnold et al. 1995; Lazarus et al. 1995; Kaiho 1998; Chapell and Peck 1999).

To efficiently analyse the morphology of randomly oriented planktic foraminifers tests with an incident light microscope, an independently operating robot was built. Here, we report on the applicability and the limitations of this new system. The system is the first step towards a fully automated robot, which also classifies and recognises particles such as foraminifers, using a neural network classifier. The current design of the system, however, enables a broad application for automated granulometry because the elementary problems of contrast and focus on an incident light microscope have been solved.

2.2 MATERIALS AND METHODS

2.2.1 Technical Description

The system consists of a CCD video camera attached to an incident light stereomicroscope equipped with a motorised stage (Fig. 2.1). It is driven by a C program running under the imaging software analySIS 3.0. Several high-level imaging functions (already available within analySIS 3.0) such as the automatic calculation of a grey-value threshold for object segmentation, detection of objects and extraction of morphological parameters, were implemented in the C-program developed at the ETH Zurich.

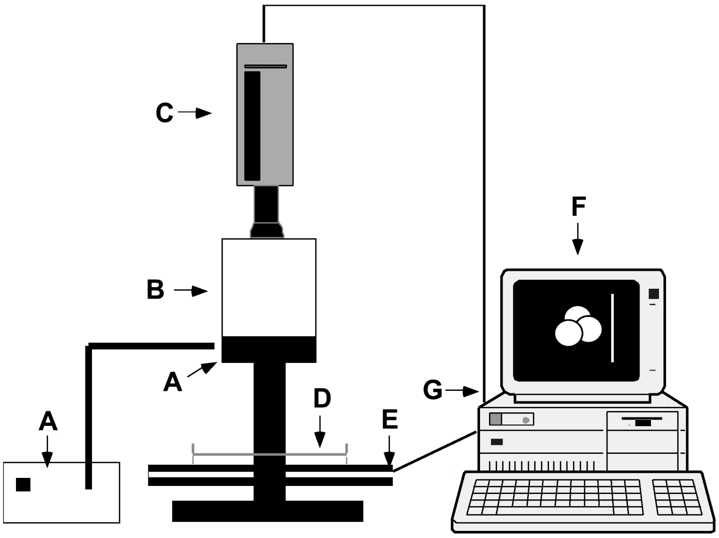

Figure 2.1: Schematic sketch of the set-up. A: Ring light; B: Microscope; C: CCD video camera; D: Glass tray with level holder; E: Computer controlled motorised X, Y — stage, F: Computer, G: Video frame grabber.

The motorised stage is controlled via a serial interface (RS232) and image capturing is done with a video frame grabber (Grabbit SIS, 16 bit, 50Hz, PAL, 768x576 pixels). If a motorised stage is used that is already supported by analySIS 3.0 (e.g. Märzhäuser L-Step 3) no extensive programming is needed. AnalySIS 3.0 provides a special extension, the automater modul, that can be used to define the automatic image analysing procedures (macros) without any further programming knowledge. All components and the suppliers are listed in Appendix 2.I.

The precision of size measurements depends on the pixel resolution of the frame grabber (here 768x576 pixels) and the applied magnification. The system can be used with magnifications ranging from 65x, with a pixel size of 8.01µm, to 400x, with a pixel size of 1.38µm. For all tests, a magnification of 160x with a pixel size of 3.31µm was used.

2.2.2 Segmentation and Focus Problems

In order to overcome elementary problems of ambiguously defined and focused objects with an incident light microscope, a low-reflectance glass tray was constructed in combination with a tray holder that enables levelling of the tray (Fig. 2.2). The glass tray is mounted about three centimetres above a black velvet cloth and held level with three adjustable feet that are attached to the tray holder (see Fig. 2.2). This design provides a homogeneous dark background (low reflectance) because the black velvet cloth below the tray largely absorbs reflected light. Therefore, bright objects can be unequivocally detected and the largest outline of an object can be automatically identified even if the contrast and/or the sharpness is very low. Levelling of the glass tray with the adjustable feet prevents that objects run completely out of the focus range over a predefined scanning area, for instance of 105 x 65 mm.

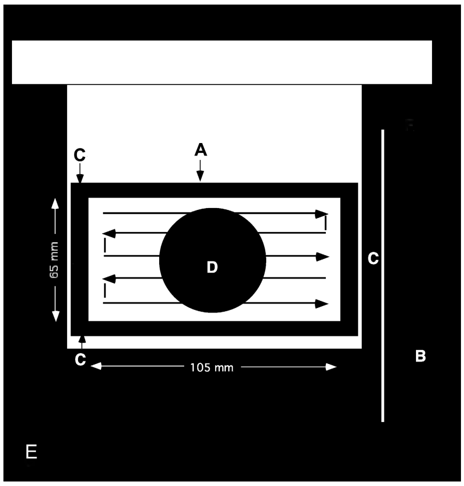

Figure 2.2: Top view of the stage set-up. Components from top to down. — A: Glass tray; B: Level tray holder; C: Three adjustable feet; D: Black velvet cloth; E: Base plate. The arrows indicate the scan track.

Widely used black painted metal trays are not suitable for automated detection of objects because light of varying intensities (depending on the light inclination) is reflected from small irregularities on the surface. Therefore, it is very difficult to calculate a grey-value threshold that can be applied for object segmentation of all objects in one field of view.

2.2.3 Working Procedure

In order to avoid measuring aggregates of particles, a small amount of material (e.g., sieved foraminifers) is evenly distributed on the glass tray. Subsequently, step size, size of the scanning area, size range of objects to be detected and sample information can be defined in an interactive set-up dialogue. The robot scans the glass tray stepwise over the predefined area (e.g., 105 x 65 mm) at a constant magnification that can be specified between 65 to 400 times (Fig. 2.2). The system captures about 1000 images per hour, sharpens them, defines the object boundaries and extracts the morphological parameters for each object, e.g., diameter, area, perimeter, mean grey values and roundness. All images of objects and their measurements are stored on a hard disk and are subsequently archived on CD-ROMs. Note — Objects that are intersected by the image border are automatically excluded from further analysis.

2.2.4 Postprocessing

Although all samples (foraminiferal sand and glass beads) were evenly distributed, aggregates of foraminifers, detrital grains, particles of the same size class, such as radiolaria and sponge spicules, may bias the results. In order to minimise these effects, several post-processing routines have been applied.

First, the roundness or shape factor measurements of particles can be used to easily distinguish between foraminifers and aggregates. The roundness was calculated as follows:

$$shapefactor = 4 \bullet \pi \bullet \frac{area}{perimeter^2}$$

For spherical particles, the shape factor is one; for all other particles, it is less than one. The smaller the shape factor is, the more elongated is the particle. The shape factor of different foraminiferal species has been determined for 212 individuals. Minimum roundness is 0.71, mean roundness is 0.90, and the maximum is 1.0. Particles with roundness factors less than a threshold value of 0.7 are either aggregates of foraminifers, broken particles, sponge spicules or tubular benthic foraminifers. All measurements of particles with roundness factors less than the threshold are excluded from further analysis.

In addition, the grey-value estimate of a particle is used to distinguish between different components, e.g., quartz grains and foraminifers. In order to apply the grey value for particle classification, light irradiance has to be constant during data acquisition. In the used set-up, foraminifers have a grey value above 100 on a scale between 0 and 255 (black and white, with a background constant 12), whereas detrital grains vary between 60 and 80.

Radiolaria and benthic foraminifers cannot be excluded from the data set because the roundness, as well as the grey values, of these organisms are comparable to those of planktic foraminifers.

Technical details can be found under http://www.geology.ethz.ch/mp/data/alfa/alfa.html

2.3 RESULTS

In order to test the accuracy and the reproducibility of measurements obtained with the new system, three different size classes of standard glass microbeads have been analysed (mean diameter with standard deviation of 168µm±7.4µm, 331µm±14.1µm, and 655µm±29.0µm, Duke Scientific co-operation). Repeated preparations and measurements of these microbeads showed a good reproducibility and an accuracy (172µm ±5.1µm; 330µm ±3.51µm; 636µm ±24.2µm) of mean diameter for all microbeads (Tab. 2.1). Comparison of manually and automatically collected measurements of the three size standards revealed no statistically significant difference (Tab. 2.1).

Furthermore, accuracy and reproducibility of repeated analysis of the same natural foraminiferal sediment sample were determined. The sample was redistributed ten times and measured at 160x magnification. The average size of the foraminiferal assemblage was 259.4 ± 4.1µm standard deviation and the median size was 230.2 ± 3.9µm standard deviation (Tab. 2.2).

Table 2.1: Reproducibility and accuracy tested with standard glass microbeads of three different diameters. N = sum of all measurements in one size class; Std = Standard deviation; 95% Conf. = 95% confidence interval; Auto = Automatically collected data; Man = Manually collected data.

Size class 168µm±8.4µm	N	Average size	Median size	Std size	95%
Auto	1691	177.80	176.75	10.18	0.49
Auto	1939	178.13	177.11	9.12	0.41
Auto	1467	175.08	173.96	8.30	0.42
Auto	1555	167.16	167.01	8.20	0.41
Auto	1320	166.22	166.12	6.73	0.36
Auto	184	171.97	172.34	7.12	1.03
Average		172.73	172.22	8.28	0.52
Standard devia-		5.18	4.73		
Man	50	170.62	170.23	7.91	0.07

Size class 331µm±10µm	N	Average size	Median size	Std size	95%
Auto	280	334.74	334.52	13.95	1.63
Auto	341	325.11	326.79	28.33	3.01
Auto	329	328.24	331.93	41.89	4.53
Auto	96	331.02	333.50	25.46	5.09
Auto	190	331.42	331.14	14.53	2.07
Auto	339	328.29	326.96	13.42	1.43
Auto	278	334.65	334.24	13.97	1.64
Average		330.49	331.30	21.65	2.77
Standard devia-		3.54	3.25		
Man	50	323.89	324.40	13.51	0.12

Size class 655µm±20µm	N	Average size	Median size	Std size	95%
Auto	95	639.54	646.34	85.39	17.17
Auto	134	641.11	655.07	96.57	16.35
Auto	132	597.53	649.00	167.06	28.50
Auto	100	652.84	652.07	20.64	4.04
Average	120	632.76	650.62	92.42	16.52
Standard devia-		24.22	3.78		
Man	50	636.35	632.75	24.56	0.21

Table 2.2: Reproducibility of ten repeated measurements of the same foraminifera sand. N = sum of all measurements in one size class; Std = Standard deviation; 95% Conf. = 95% confidence interval; Auto = Automatically collected data.

Sand	N	Average size [µm]	Median size	Std size	95%
Auto	184	260.33	231.37	79.80	3.64
Auto	168	257.31	229.71	76.05	3.63
Auto	148	255.47	228.49	76.29	3.88
Auto	151	261.85	233.30	79.73	4.01
Auto	159	257.87	226.24	83.76	4.11
Auto	152	262.06	230.41	83.11	4.17
Auto	143	264.42	234.73	83.29	4.31
Auto	142	265.97	237.02	81.82	4.25
Auto	172	253.97	225.91	77.28	3.65
Auto	164	254.95	225.24	78.67	3.80

Size	[µm	259.42	230.24
Standard	[µm	±4.13	±3.94
Standard	[%]	±1.59	±1.71
95%		0.1	0.09

2.4 DISCUSSION AND CONCLUSIONS

The tests revealed highly accurate and reproducible results for particle size. However, the amount of material used strongly influences the formation of aggregates that might falsify the result. Therefore, we recommend using a small amount of material for the analyses. If size and shape of a single particle group is analysed, for example planktic foraminifera, additional post processing has to be done to avoid measuring particles other than planktic foraminifera. The grey-value distribution and the roundness can be used to distinguish foraminifera from other particles. However, radiolarians and round benthic foraminifera cannot be separated.

The new robot offers the opportunity to collect a large number of reliable morphological measurements within a short time using an incident light microscope. The elementary problems of contrast and focus on an incident light microscope were solved using a low-reflectance and levelled glass tray. Therefore, it is expected that the system can be applied to all kinds of grain size and shape analyses in the size range from 63µm to 2000µm. In order to increase the efficiency of the data collection, we are currently using a system that analyses six samples in a batch process (Fig. 2.3). The system will be extended by a) a neural network classifier that enables on-line recognition of particles and b) a picking device for the collection of objects.

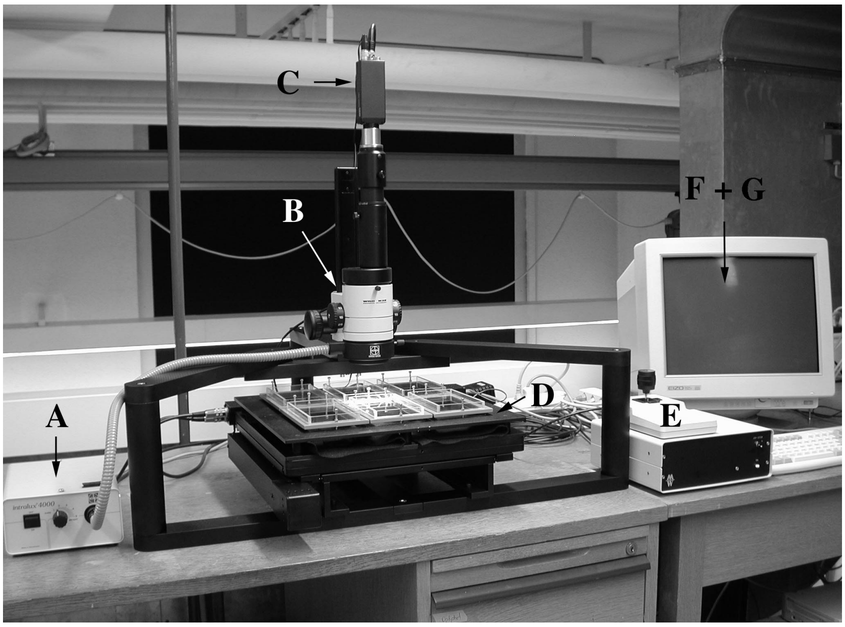

Figure 2.3: Currently used system that analyses six samples in a batch process. A = light source, B = microscope, C = video camera, D = motorized stage, E = control module for stage, F+G = computer with frame grabber.

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CHAPTER 3*

SIZE DISTRIBUTION OF HOLOCENE PLANKTIC FORAMINIFER ASSEMBLAGES: BIOGEOGRAPHY, ECOLOGY AND ADAPTATION

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ABSTRACT

The size of any organism is influenced by the surrounding ecological conditions. In this study, we investigate the effects of environmental factors on the size spectra of planktic foraminiferal assemblages from Holocene surface sediments. We analysed assemblages from 69 Holocene samples, taken from locations which represent the major physical and chemical gradients of the oceans. It appears that temperature, primary productivity and seasonality are the main driving forces for the observed size pattern. On a global scale, the size spectra of assemblages triple from the poles to the tropics. Smaller sizes are associated with the polar and subtropical fronts, at 2°C and 17°C respectively, as well as in upwelling areas. On a regional scale, primary productivity is the driving force for the size signal. Apart from entire assemblages, the relationships between test size, temperature and the influences of perturbations, such as frontal systems, can also be seen at the species level.

3.1 INTRODUCTION

The size of an organism is an obvious morphological characteristic and is easy to quantify. Consequently, it has been studied extensively in numerous groups of organisms (Futuyma 1998). Much of this work was focused on terrestrial organisms, showing both the role of ecology (Bergmann's rule, i.e. increase in body-size towards high latitudes) and evolution (Cope's law, i.e. increase in body-size along a lineage). Fewer studies have addressed the factors influencing size of marine organisms. Recent research has identified oxygen availability as controlling size in amphipods (Chapelle and Peck 1999), benthic foraminifers (Kaiho 1998), and gastropods (McClain and Rex 2001).

Planktic foraminifers, because of their wide geographical occurrence, allow global studies of ecological and evolutionary influences on size. Size changes in modern planktic foraminiferal species have been related to ecological factors such as temperature (Bé et al. 1973; Hecht 1976) and upwelling intensity (Naidu and Malmgren 1995). From an evolutionary point of view, foraminifers as a group have undergone at least three periods of diversification since their origin in the Mid-Jurassic (Loeblich and Tappan 1985), each of which is thought to have involved a general increase in test size (Arnold et al 1995).

Most studies of evolutionary size changes in planktic foraminifers focused on single species or lineages (e.g. Malmgren and Kennett 1981; Arnold 1983; Malmgren et al. 1983; Spencer-Cervato and Thierstein 1997; Kucera and Malmgren 1998; MacLeod et al. 2000). Such studies on single species analyses have provided regional ecological and stratigraphic information on size change. Studying entire planktic foraminiferal assemblages in addition to single species holds the potential to give insights into long-term macro-evolutionary processes or potential global environmental changes. The only previous attempt to study Cenozoic size variation of the entire group of planktic foraminifers (Gould; 1988, Norris 1991; Arnold et al. 1995; Parker et al. 1999) was based on analyses of one specimen per species, restricting the reliability of the results.

In order to understand the ecological significance of size variability we have studied planktic foraminifer assemblages in a Holocene data set as a first step towards an analysis of size changes of planktic foraminifers in the late Phanerozoic. We propose that the test sizes of total planktic foraminiferal assemblages are the result of various processes acting on at least three different scales. (1) Globally all foraminifers might be influenced by the physical and chemical properties of the ambient sea water, such as temperature, salinity, nutrient availability, carbonate saturation, and oxygen availability (e.g. Berger 1969; Bé and Tolderlund 1971; Caron et al. 1981; Caron et al. 1987a; Bijma et al. 1992; Schiebel et al. 2001). If so, size might depend on these factors on a global scale – a testable hypothesis. (2) Biogeographic differences in species composition and diversity have been well documented (Bé and Tolderlund 1971; Hemleben et al. 1989). Since individual species show distinct size variability (Hecht 1976), biogeographic changes in species composition may lead to size changes of the entire assemblages. (3) Test sizes of populations of individual species are known to vary with environmental factors (Hecht 1976; Ortiz et al. 1995; Naidu and Malmgren 1996) with size maxima at distinct environmental conditions. Size-changes of the entire planktic foraminiferal assemblages may therefore represent a composite of size spectra of various species, which may have lived at or outside their environmental optima. These spectra reflect the evolutionary influence on the basic size of the species.

3.2 MATERIAL AND METHODS

3.2.1 Material

We have identified a set of 69 suitable surface sediment samples (Fig. 3.1) covering all biogeographic zones which were defined based on the species composition of planktic foraminifers (Bé and Tolderlund 1971; Hemleben et al. 1989).

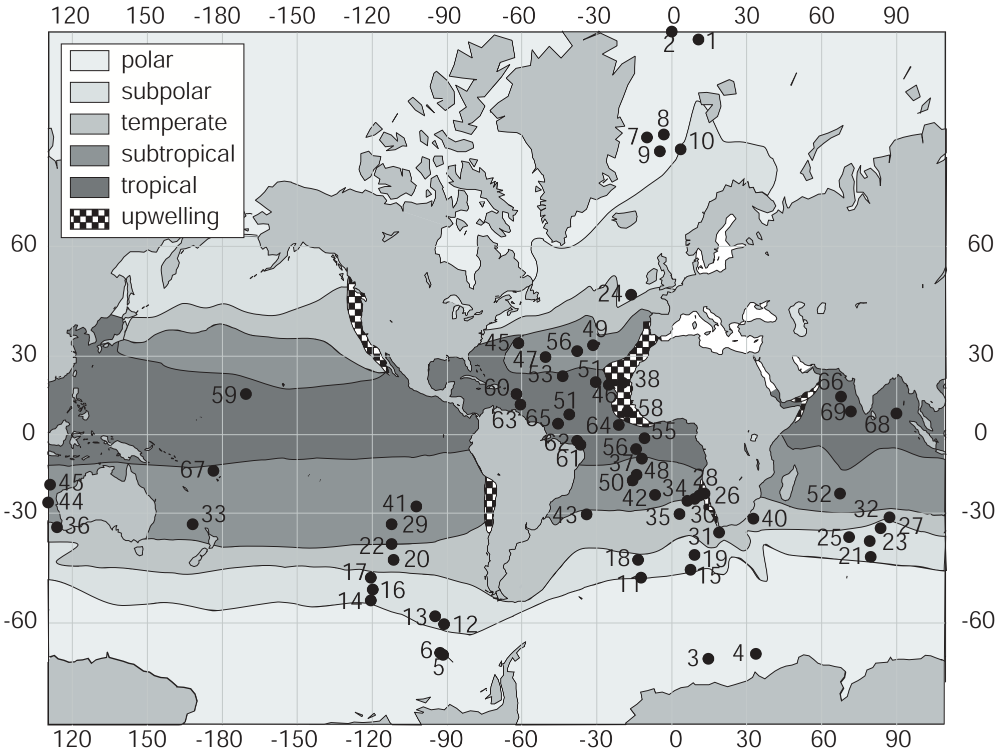

Figure 3.1: Sample locations. Biogeographic areas are based on Bé and Tolderlund (1971) and Hemleben et al. (1989). Negative values refer to southern latitude respectively to western longitude.

They are from water depths of 808 to 4825m (with a mean of 3000m) and show no signs of dissolution and few non-foraminiferal particles. The samples cover the major physical and chemical gradients of the world’s oceans (Appendix 3.I). The fraction larger than 150 µm was used for analysis to allow for species recognition on digitized images and to exclude pre-adult ontogenetic changes in test form (Brummer et al. 1987). Using the same as size fraction as the global taxonomic data set of Prell et al. (1999) also allows direct comparison with their relative abundance data.

3.2.2 Size Measurements

A representative split of a mean of 1667 individuals was measured within each assemblage (minimum 685, maximum 3797 individuals), in a total of 114991 measurements. The acquisition of such a large morphometric data set was possible because we used a system for automated test outline extraction. The system consists of a CCD video camera attached to an incident light stereomicroscope equipped with a motorized stage (Bollmann et al. subm). Foraminifers are strewn on a glass tray and are, hence, not oriented. A predefined area was scanned and all images were saved. The maximum diameter of the object was chosen as the most suitable size estimator because it is least affected by random orientation. The accuracy of diameter determination at the applied magnification of 160x is 3.31 µm per pixel.

Aggregates, detrital grains, pteropods and sponge spicules could be identified based on their distinct gray values and shape factors (perimeter to area ratio) and removed from the data set. Base on these parameters, benthic and planktic foraminifers and carbonated grains of comparable size and shape could not be distinguished. Since benthic foraminifers usually make up less than 1% of a well-preserved deep-sea sample, their contribution is considered to be tolerable.

3.2.3 Data Analysis

To characterize the size distribution of the assemblage, the mean, median, the 95-percentile and the maximum were determined. The precision of the size determination of entire assemblages was determined by repeated measurements of the same sample. The errors are estimated at ±1.6% (two standard deviations) for the mean, ±1.7% for the median and ±2.2% for $\text{size}_{\text{assemblage5}}$. To describe the size changes of individual species within the largest 5% of the assemblages, the term “$\text{size}_{\text{species5}}$” is used.

Natural foraminifer populations, because of their serial chamber additions, must start with the largest number of individuals in the size class of the first chamber, which ranges from 7 to 35 µm

(Hemleben 1989). Because of differential mortality, the size distribution may deviate from an exponentially decreasing size distribution. The minimum size in our data set is given by the sieve size (>150µm), represents an artificial cut-off of the natural size distribution, and therefore does not have any biological significance. Since the distributions are highly skewed towards large size (Fig. 3.2), the best descriptor of the distribution are the size$_{\text{assemblage5}}$ and the maximum. Of these two, sizes$_{\text{assemblage5}}$ show high correlation with means, medians, and maxima (for the mean r = 0.942, median r = 0.817, maximum r = 0.886, for all correlations p = 0.000). The maximum, dependent on random sampling bias, has a lower correlation with mean and median than the size$_{\text{assemblage5}}$. To evaluate the potential effects of species changes, the largest 5% of the assemblage were taxonomically classified in 17 environmentally representative samples and the mean size for each species "size$_{\text{species5}}$" was calculated (Appendix 3.III). Additionally, in all assemblages the 12 largest individuals were taxonomically classified to determine the environmental conditions for maximum size development of individual species.

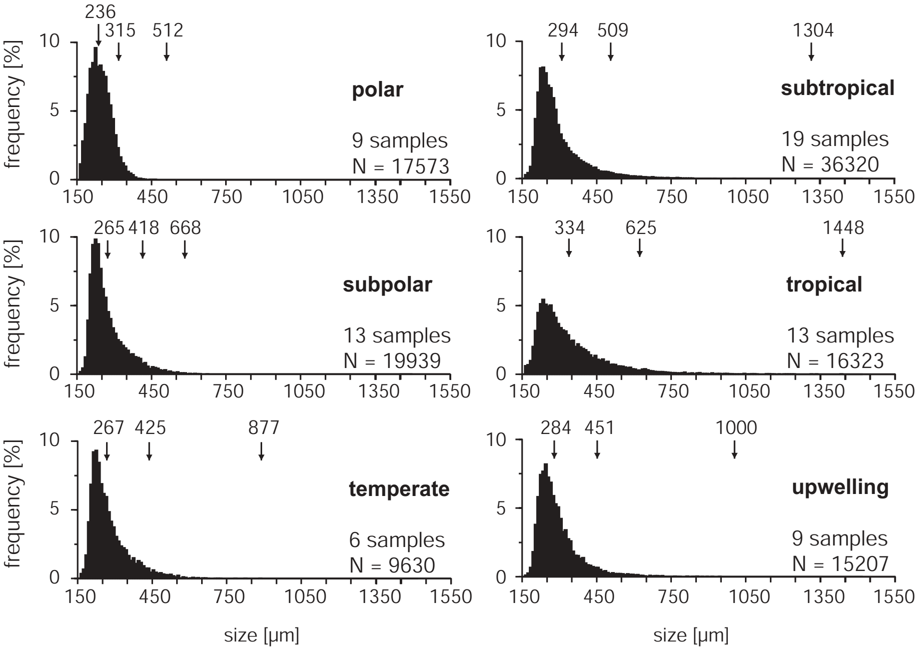

Figure 3.2: Size distribution within biogeographic zones. The distribution shows measurements of all individuals within a biogeographic zone. The arrows indicate, from the left to the right, average, 95-percentile and maximum of the zonal distribution with the corresponding values, N = number of measurements.

The environmental data used in our analyses are annual mean sea-surface temperature and primary productivity. The significance of these two parameters was confirmed in multivariate statistical analyses of numerous parameters (annual mean temperature, maximum seasonal temperature difference at 0 m, salinity, dissolved oxygen, nitrate, phosphate, and silicate (annual means at 0 m and 200 m and the difference between these depths) as well as primary productivity (annual mean, seasonal minima and maxima), all taken from Levitus et al. (1994) and Antoine et al. (1996).

The relationship between $\text{size}_{\text{assemblage5}}$ and the environmental characteristics was analysed by linear correlation and by forward multiple linear regression. The lowest probability tolerated in the analysis was $p = 0.05$. The differences within biogeographic zones were tested by an analysis of variance (ANOVA) on $\text{size}_{\text{assemblage5}}$. Within a biogeographic zone, the relationship between size and environmental parameters was re-analysed by linear correlation analysis. Linear correlation analysis was chosen because of the reduced number of samples per zone.

3.3 ENVIRONMENTAL SETTING

The structure of all environmental measurements was analysed by a Principal Component Analysis (Tab. 3.1).

Table 3.1: Factor loadings of the Q-mode principal component analysis. Index 0 refers to the sea surface, index 200 to 200 meter depth, D to the difference between 0 and 200 meters. Data analysed: average annual temperature (T_0) (T_{200}) (ΔT), salinity (Sal_0) (Sal_{200}) (ΔSal), annual concentrations of oxygen (Ox_0) (Ox_{200}), phosphate ($PO_{4\ 0}$) ($PO_{4\ 200}$) (ΔPO_4), nitrate ($NO_{3\ 0}$) ($NO_{3\ 200}$) (ΔNO_3), minimum (t_{min}) and maximum (t_{max}) annual surface temperature, maximum difference of monthly temperatures (t_{seas}) (all physico-chemical environmental data from Levitus (1994). Annual primary productivity (PP_{ann}), seasonal maximum and minimum primary productivity (PP_{max}, PP_{min}), difference between the previous values of primary productivity (PP_{seas}), primary productivity in spring (April to June at the northern Hemisphere, October to December at the southern Hemisphere)(PP_{spring}) and winter (January to March at the northern Hemisphere, July to September at the southern Hemisphere) (PP_{winter}) (all primary productivity data from Antoine et al. (1996). Highest factor loadings are marked in bold.

	F1	*F2*	*F3*
t_0	0.946	0.264	-0.105
Sal_0	0.727	0.366	0.201
Ox_0	-0.932	-0.303	-0.080
$PO_{4\ 0}$	-0.299	-0.589	0.313
$NO_{3\ 0}$	-0.714	-0.267	-0.161
t_{200}	0.860	-0.421	0.106
Sal_{200}	0.718	-0.281	0.298
Ox_{200}	-0.861	-0.195	0.395
$PO_{4\ 200}$	0.208	0.549	0.460
$NO_{3\ 200}$	-0.294	0.543	-0.640
Δt	0.838	0.041	-0.390
ΔSal	0.457	-0.294	0.046
ΔOx	0.256	0.673	-0.535
ΔPO_4	-0.306	-0.428	-0.409
ΔNO_3	-0.395	-0.442	0.691
T_{min}	0.942	-0.230	-0.163
T_{max}	0.946	-0.289	-0.061
t_{seas}	0.095	-0.357	0.580
PP_{ann}	0.714	0.614	0.220
PP_{max}	0.527	0.760	0.265
PP_{min}	0.874	0.363	0.060
PP_{seas}	-0.121	0.780	0.361
PP_{spring}	0.854	0.393	0.093
PP_{winter}	0.491	0.725	0.242
Eigenvalue	10.57	5.16	2.83
expl. Variance	44.05	21.05	11.79

The first axis (44% of total variance) showed the highest correlations with sea-surface temperature (annual mean and annual maximum: r = 0.95) and the second axis (21% variance) with primary productivity (annual mean, r = 0.61; maximum, r = 0.76). The analyses of the size response to environmental change consequently were focused on mean sea-surface temperature and maximum primary productivity.

The biogeographic zones were defined based on the changing species composition of living planktic foraminifers (Bé and Tolderlund 1971; Hemleben et al. 1989). The relationship between temperature and primary productivity is different in polar to temperate biogeographic zones than in the subtropical and tropical zones. The zones are structured, with only small overlaps, along the global temperature gradient (Fig. 3.3).

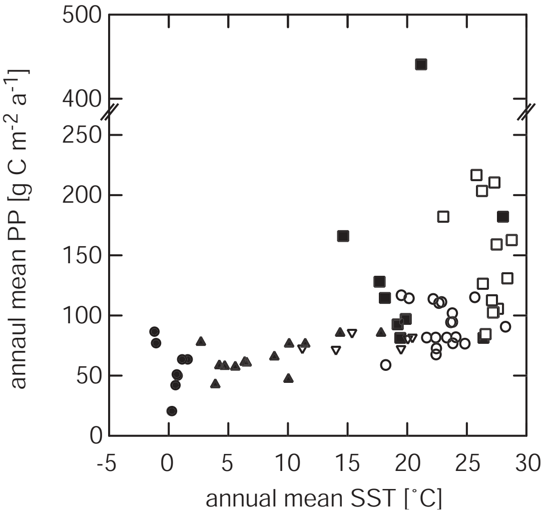

Figure 3.3: Temperature (°C) versus primary productivity (g C $m^{-2}a^{-1}$) for all samples. Biogeographic zones are polar (filled circle), subpolar (filled triangle), temperate (open triangle), subtropical (open circle), tropical (open square), upwelling (filled square) are indicated.

Superimposed are the effects of primary productivity, describing two different temperature-fertility relationships (Fig. 3.3). From the subpolar to temperate zones, fertility gradually increases with temperature, whereas in the subtropical and tropical zones variability of primary productivity increases dramatically within relatively small temperature intervals. A large fertility and a limited temperature gradient characterize the upwelling zone.

3.4 RESULTS AND INTERPRETATION

3.4.1 General Size Distribution

The size distributions of all analysed planktic foraminiferal assemblages are strongly skewed towards larger sizes (Fig. 3.2). From the polar to the tropical zone, the size$_{\text{assemblage5}}$ doubles, from 315 to 625 µm and the maximum test size almost triples from 512 to 1448 µm. The upwelling assemblages have size distributions most similar to the temperate and subtropical ones. To analyse these patterns in more detail, the relationship of the size$_{\text{assemblage5}}$ with the main environmental parameters is further investigated. The mean size$_{\text{assemblage5}}$ for the six biogeographic zones are highly correlated (r = 0.938, *p* = 0.006) with temperature (Fig. 3.4). However, compared to the general linear increase of the size$_{\text{assemblage5}}$ from the polar to the tropical zones, the upwelling group is an outlier and shows a smaller size than expected.

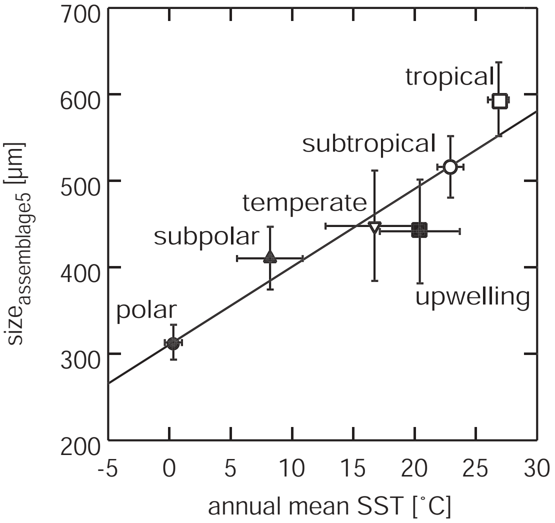

Figure 3.4: Size$_{\text{assemblage5}}$ per sample (µm) plotted against mean annual sea-surface temperature (SST in °C) from Levitus, World Ocean Atlas (1994). Arrows indicate the areas of minimum size at 2°C and 17°C, corresponding to the polar and subtropical front, respectively. The black line represents the 5-point moving average. Biogeographic zones as in Fig. 3.3

An examination of the size/temperature relationship of the individual assemblages shows that the increase of the sizes$_{\text{assemblage5}}$ is not monotonous but shows two distinct local minima at sea surface temperatures of around 2°C and 17°C sea surface temperature (Fig. 3.5). Next to the annual mean sea-surface temperature, the difference of annual temperatures at the sea surface and in 200 meters depth, which indicate the stratification in the upper water column, show a high correlation with sizes$_{\text{assemblage5}}$.

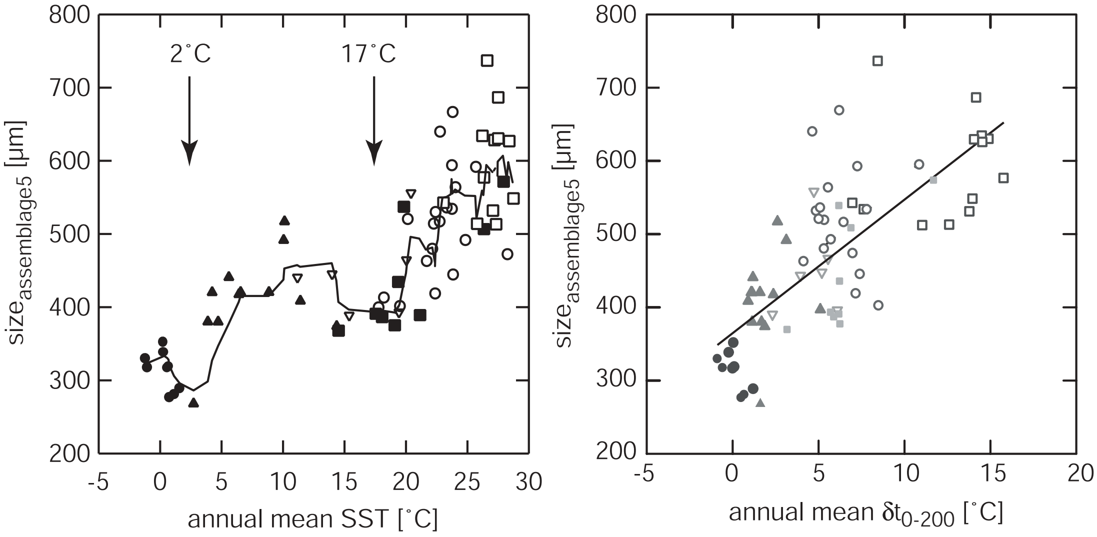

Figure 3.5: Size$_{assemblage5}$ per sample (µm) plotted against mean annual sea-surface temperature (SST in °C) (left) and difference between mean annual sst and temperature at 200 meters depth. Temperature are from Levitus, World Ocean Atlas (1994). Arrows indicate the areas of minimum size at 2°C and 17°C, corresponding to the polar and subtropical front, respectively. The black line represents the 5-point moving average (for the left graph) and the linear fit for the right graph. Biogeographic zones as in Fig. 3.3

Table 3.2: Correlation coefficient matrix (r) for the environmental parameters and size$_{assemblage5}$ for the global data set and for the different biogeographic zones. Abbreviations and references see tab. 3.1. Significant correlation is marked in bold.

	global	polar	subpolar	temperate	subtropical	tropical	upwelling
T 0 m	**0.793**	-0.546	0.273	0.374	0.380	0.181	**0.784**
Sal 0 m	**0.499**	-0.112	-0.330	0.412	0.198	-0.177	0.473
Ox 0 m	**-0.770**	-0.148	-0.315	-0.345	-0.249	-0.091	**-0.772**
PO_4 0 m	**-0.404**	**0.857**	0.243	-0.288	-0.022	-0.412	-0.440
NO_3 0 m	**-0.439**	0.590	0.292	-0.141	-0.297	-0.481	-0.559
T 200 m	**0.683**	-0.192	0.260	0.343	0.230	-0.064	0.609
Sal 200 m	**0.453**	-0.463	-0.362	0.451	0.385	**-0.588**	0.183
Ox 200 m	**-0.675**	**-0.851**	-0.323	-0.562	-0.430	0.088	-0.374
PO_4 200 m	-0.071	**0.714**	0.255	-0.210	-0.200	-0.325	-0.436
NO_3 200 m	-0.114	0.542	0.281	0.026	0.215	0.075	0.089
ΔT 0-200m	**0.740**	**-0.673**	0.203	0.203	0.019	0.137	**0.740**
T_{seas}	-0.140	**-0.749**	-0.100	0.273	-0.032	-0.424	0.091
PP_{ann}	**0.283**	-0.408	-0.252	0.155	0.325	-0.442	-0.202
PP_{seas}	**-0.378**	-0.382	**-0.716**	-0.394	0.372	-0.284	-0.272
PP_{max}	0.103	-0.385	**-0.654**	-0.445	**0.500**	-0.450	-0.207
PP_{min}	**0.504**	0.099	0.371	0.059	0.389	**-0.628**	-0.107
PP_{spring}	**0.472**	0.099	0.357	0.059	0.389	**-0.591**	-0.179
PP_{winter}	0.059	-0.588	**-0.654**	**-0.818**	0.243	-0.434	-0.200

A multiple linear regression analysis of the $\text{size}_{\text{assemblage5}}$ with all environmental parameters available revealed the strongest influence of mean sea surface temperature (63% of the size variance explained), followed by seasonality of temperature (+ 4%), and fertility (+ 1%): $\text{size}_{\text{assemblage5}} = 9.626t_0 - 14.297t_{\text{seas}} - 0.945\text{pp}_{\text{winter}} + 391.671$; $r = 0.833$, $p = 0.000$). On the global scale primary productivity and temperature show a strong positive correlation, which is the reason for the small variance explained by primary productivity (Appendix 3.II). To reduce the globally dominant influence of temperature, the data set was split into biogeographic zones, within which the effects of secondary factors, such as primary productivity might be better recognizable.

3.4.2 Size Patterns within Biogeographic Zones

The multiple linear regression equation discussed above points to a negative influence of primary productivity on size. Moreover the mean $\text{size}_{\text{assemblage5}}$ of the upwelling assemblage is distinctly smaller than expected from the global size/temperature correlation (Fig. 3.4). On the other hand, an increase in the mean test sizes of several planktic foraminiferal species in Quaternary cores has been linked to higher paleo-fertility in the Arabian Sea (Naidu and Malmgren, 1995).

As evident in Figure 3.3 there is little correlation between primary productivity and temperature within the individual biogeographic zones except in one. The exception is the subpolar zone with a positive correlation between the annual mean primary productivity and sea surface temperature. Therefore, any size trend in this zone could be related to either parameter. Within all other zones, a size dependency on fertility, which is unrelated to temperature, might be identifiable.

A linear correlation analysis of size and environment within individual biogeographic zones shows that in subpolar, temperate and tropical assemblages size is negatively correlated to primary productivity (Tab. 3.2), whereas in the subtropics the correlation is positive. In the polar assemblage there is no significant correlation with primary productivity, but there is a strong positive correlation with another fertility parameter, i.e., the nutrient phosphate. Within the upwelling zone the $\text{size}_{\text{assemblage5}}$ shows the highest correlation coefficient not with a fertility parameter, but with sea surface temperature (Tab. 3.2). Contrary to the definition of all other biogeographic zones, which are dominantly based on temperature criteria, the upwelling assemblage is defined by the dominance of the species *G. bulloides*, which has an affinity to high nutrients in a wide range of water temperatures (Hemleben, 1989). Because fertility is the dominant characteristic of assemblage definition, temperature is the dominant variable within this heterogeneous zone.

The inconsistent size relationship with fertility among the biogeographic zones defies a simple explanation. Since biogeographic zones are defined by the dominance of a few species, it is likely that successive adaptational optima of these might strongly influence the observed assemblage patterns.

3.4.3 Size Effects Related to Changing Species Abundances

Size Variation and Diversity

Changing $\text{size}_{\text{assemblage5}}$ are a composite result of size variability within species and among species (Hecht, 1976), the number of species, and their changing abundance. It has repeatedly been documented that species richness in planktic foraminifers increases from low to high temperatures (Bé and Tolderlund, 1971; Rutherford et al., 1999). A larger number of species in an assemblage also increases the probability of including large species (statistical effect). In our data set, assemblage size is indeed correlated with species richness ($r = 0.598$, $p = 0.000$). Whether this correlation is just a statistical effect or is caused by the fact that warm-water species are larger and become more abundant requires an examination of size distribution patterns in individual species.

Size Variation at the Species Level

We have investigated in our subset of 17 representative samples the $\text{size}_{\text{species5}}$ of the largest 5% of the assemblages (Appendix 3.III). This fraction included an average of 80 specimens per sample, in which we found a total of 23 species. The occurrences for only 12 of these were consistent enough for a comparison, i.e. they were present with more than 5 specimens in at least two samples. These species are polar *Neogloboquadrina pachyderma*, subpolar and temperate *Globigerina bulloides*, *Globorotalia truncatulinoides*, *G. inflata*, *Orbulina universa*, and subtropical to tropical species *Globorotalia hirsuta*, *G. menardii*, *G. tumida*, *Globigerinoides ruber*, *G. sacculifer*, *G. conglobatus* and *Pulleniatina obliquiloculata*.

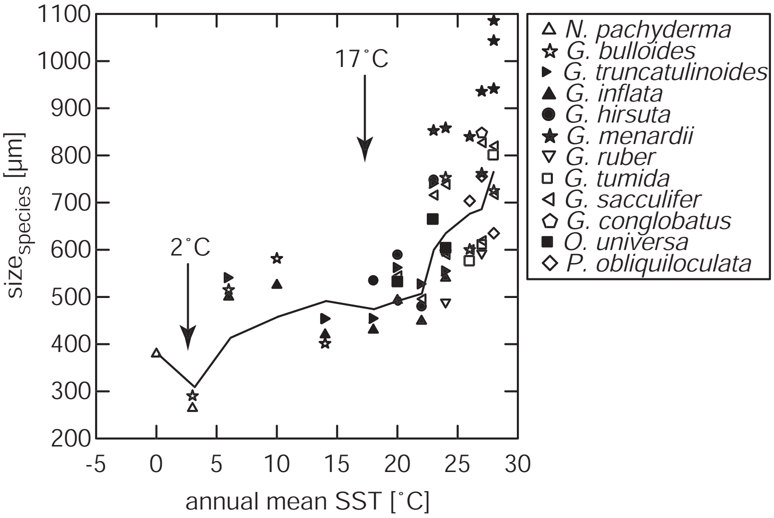

Figure 3.6: Average size (µm) of the dominant species within the largest 5% of the assemblage (size$_{species5}$) plotted against mean annual sea-surface temperature (SST in °C) from Levitus, World Ocean Atlas (1994). Arrows indicate the areas of minimum size at 2°C and 17°C, corresponding to the polar and subtropical front, respectively. The black line represents the 5-point moving average.

A global plot of all means of these sizes$_{species5}$ (Fig. 3.6) shows a similar temperature-related increase as the size$_{assemblage5}$. Size patterns of individual taxa also reproduce the two assemblage size minima at 2-3°C and 17°C. Apparently three levels of maximum size development can be distinguished. Small species, such as *N. pachyderma* (and likely *T. quinqueloba*) live in polar waters and reach a maximum diameter of less than 500 µm. Medium-sized species, such as *O. universa*, *G. truncatulinoides*, *G. inflata,* reach 500 to 1000 µm in subpolar to tropical zones. Similar maximum sizes of *G. ruber*, *G. hirsuta* and *G. conglobatus* are only attained in the subtropics and tropics. The largest species, which are characteristic of the tropical zone, may grow to 1300 µm (*G. tumida* and *G. sacculifer*) or even 1500 µm (*G. menardii*). Because the tropics host species that may grow to large and intermediate sizes, the total variability of size$_{assemlbage5}$ is also large. In temperate waters, the maximum sizes obtained for all species, and thus the assemblages, are surprisingly similar.

Our data allow us to identify characteristic temperatures at which the largest size and relative abundance of individual species coincide globally (Fig. 3.7). These temperatures define four groups of species with ecological optima in polar, temperate, subtropical, and tropical zones. These are polar species *N. pachyderma* (sinistral) around 0°C; typical temperate species *G. bulloides* and *N. pachyderma* (dextral) around 12 °C, subtropical (20 - 25°C) with deep-dwelling species *G. inflata*, *G. truncatulinoides*, *G. hirsuta* and additionally *O. universa*, and tropical (>25°C) with the surface dwellers *G. menardii*, *G. ruber*, *G. sacculifer*, *G. conglobatus* and the deeper dwelling *G. tumida* (Tab. 3.3). No analysed species has its optimum size development at temperatures characteristic of frontal areas at 2° and 17°C. The size minima observed in frontal zones suggest that these assemblages consist of species living outside their ecological optima.

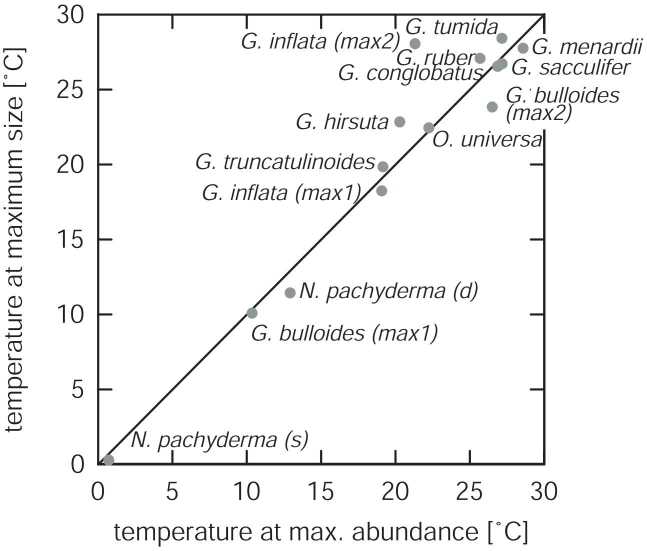

Figure 3.7: Temperature at global maximum relative abundance (Prell, 1999) and temperature at maximum size (this study). The line represents the 1:1 relationship (r = 0.963, p = 0.000).

Table 3.3: Maximum size under optimum temperature conditions (T_{opt}). $^{a)}$ Bé and Tolderlund (1971) used plankton tows >200 µm and did not mention any temperature definition; $^{b)}$ Hecht (1976) used winter temperatures and sediment samples >250 µm. and distinguished *G. truncatulinoides* left from *G. truncatulinoides* right$^{1)}$ as well as *G. ruber* white from *G. ruber* pink$^{2)}$; for comparison the data has been pooled in the present study. Our study as well as the Brown Foraminiferal Database (Prell et al. 1999) is based on sediment samples >150 µm.

Species name	T_{opt} (°C)	T_{opt} (°C)	Maximum size	Max rel. abun
N. pachyderma (s)	0 - 4	0 - 5	475/00.3	98.0/00.7
N. pachyderma (d)	10 - 18	6 - 15	591/11.4	48.4/12.9
G. bulloides	03 - 19	4 -10	718/10.1	60.1/10.3
O. universa	17 - 23	-	920/22.4	32.3/22.2
G. truncatulinoides	17 - 22	10 - 22 $^{1)}$	837/19.8	18.8/19.2
G. inflata	13 - 19	-	664/18.2	56.8/18.5
G. tumida	-	-	1253/28.4	11.8/27.2
G. menardii	20 - 25	-	1448/27.5	42.5/28.6
G. sacculifer	24 - 30	-	1228/26.6	38.1/27.2
G. ruber	21 - 29	20 - 26 $^{2)}$	974/27.5	81.0/25.8
G. hirsuta	17	-	889/22.8	8.7/20.3
G. conglobatus	21 - 29	-	1110/27.0	11.3/28.0

Additionally, we analysed the influence of changing primary productivity on the size of species (Fig. 3.8). The upper size range of the species contribution to the size$_{\text{assemblage5}}$ with primary productivity up to 150 g C m^{-2}a^{-1}. Above this threshold value, the size of species decreases with increasing primary productivity, indicating that theses species are already beyond their optimum primary productivity conditions.

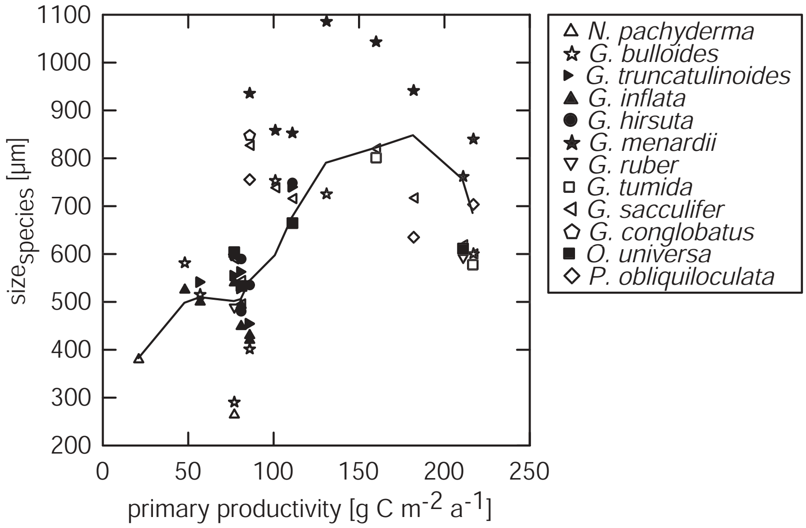

Figure 3.8: Average size (µm) of the dominant species within the largest 5% of the assemblage plotted against annual primary productivity (g C m^{-2}a^{-1}) from Antoine et al. (1996). The black line represents the 5-point moving average.

3.5 DISCUSSION

3.5.1 Latitudinal Size Variations: Possible Environmental Factors Causing the General Size Increase

Temperature

The most important trend emerging from our results is the general increase in planktic foraminiferal test size from the poles to the tropics (Figs. 3.4 and 3.5). Besides the possible direct influence of water temperature, many other ecological parameters co-vary with temperature. Cell physiology in general is known to accelerate with temperature and enzymatic activity has been shown to approximately double when temperature increases by 10°C in different species of planktic foraminifers (Caron et al. 1987a, b; Bijma et al. 1990b; Spero et al. 1991). The increasing enzymatic activity with rising temperature will lead to faster growth by enhanced calcification and cytoplasm synthesis, both of which are highly correlated (Spero et al. 1991).

Carbonate Supersaturation

Shell calcification processes depend not only on the enzymatic activity but also on the availability of Ca^{2+} ions and the amount of dissolved inorganic carbon (Gattuso et al. 1998; Bijma et al. 1999). Carbonate supersaturation is known to increase from the poles to the tropics (Buddemeier and Fautin 1996), because CO_2 is less soluble in warmer waters. Enhanced calcification in foraminiferal tests could be a direct consequence of higher carbonate supersaturation. Other symbiont-bearing organisms, such as corals, are also known to increase their size with increasing carbonate supersaturation (Gattuso et al. 1998). To our knowledge, no global data set of calcium carbonate supersaturation with appropriate spatial resolution and depth penetration exists. Such a data set would be useful to disentangle the effects of carbonate supersaturation and temperature and complementing the experimental results of Lea et al. (1996) which show higher calcification with increasing supersaturation. Additionally, changing species richness, replacement of species with different ontogenetic size trajectories, and intraspecific size changes are examples of biotic processes which could be evaluated using our data set.

Diversity

The increase in species richness from the poles to the tropics shows the same trend as the $\text{size}_{\text{assemblage5}}$, which in any single sample is the cumulative result of distinct temperature adaptations of individual species. Hence, the increase of taxa with distinct temperature-dependent size and abundance maxima, from the polar to tropical areas, could produce the observed, stepped global size increase. The observed large intra- and interspecific size variability in the tropics and subtropics, compared to the subpolar and temperate assemblages (Figs. 3.5 and 3.6), could be the result of enhanced fine-scale or short-term environmental variability. This could be related to the strong thermal gradients in the upper part of the water column and the large variability of primary productivity conditions in the tropics. Over evolutionary timescales, this may have led to an efficient ecological segregation of planktic foraminiferal species and higher diversity (Rutherford et al. 1999).

Species replacement

The subtropical and tropical environments apparently promote the growth of larger test sizes through the combined effects of higher temperatures, enhanced calcium carbonate supersaturation and high light intensity. All of these facilitate enhanced photosynthesis of symbionts and, thus, more intense harvesting by the foraminifers. Interestingly, symbiont-bearing species, such as *G. ruber*, *G. sacculifer*, and *G. conglobatus*, do indeed obtain larger maximum sizes than the asymbiotic species *N. pachyderma*, *G. bulloides*, *G. inflata*, and *G. truncatulinoides*. Symbiont-bearing species are also the most frequent components of subtropical and tropical assemblages (Hemleben et al. 1989). This fact alone could explain the larger sizes observed in these zones because enhanced symbiotic activity was experimentally shown to increase the shell size (Bé et al. 1982).

Size variation within populations.

The test size of planktic foraminifers increases during their lifetime. The final size is determined by reproduction, during which gametes are released and the empty test sinks to the ocean floor. Reproduction is known to be triggered by the synodic lunar cycle (Spindler et al. 1979; Bijma et al. 1990a; Schiebel et al. 1997) and the time allotted for growth is influenced little by local environmental conditions. However, a single specimen can grow to different adult sizes, depending on the environmentally dependent growth rates (Caron et al. 1981; Caron et al. 1987a; Bijma et al. 1990b). From these observations, we infer that larger size and a high abundance define optimum conditions, whereas small sizes and fewer numbers of individuals of a species population result from unfavourable conditions. Our results confirm the hypothesis put forward by Hecht (1976) who observed larger test sizes in the abundance maxima. For example, *G. bulloides* shows the largest sizes around 50°N, whereas the subtropical to tropical *G. ruber* attain their maximum sizes around 10°N (Hecht, 1976; tab. 3.3). Malmgren and Kennett (1976) also have described the correlation of size and frequency of *G. bulloides* in surface sediments with optimum conditions between 6-10°C, similar to our results. A correlation of size and accumulation rates of several species was documented for *Neogloboquadrina dutertrei*, *G. ruber*, *G. sacculifer* and *G. bulloides* in the Arabian Sea (Naidu and Malmgren 1995). Their data demonstrate that increased production and accumulation of tests, and not changing relative abundances, produced their size-frequency relationship.

3.5.2 Deviations from the Latitudinal Trend: Frontal Systems and Upwelling Areas

The general $\text{size}_{\text{assemblage5}}$ increase towards the tropics is not monotonous (Fig. 3.5). Instead, deviations from the general trend indicate the influence of secondary factors, which interfere with the global temperature–related effects. Smaller sizes are found at sea surface temperatures around 17°C and 2°C. These temperatures define two of the most important frontal systems, the subtropical fronts, which are associated with 15- 18°C sea-surface temperatures, and the northern and southern polar fronts, which are characterised by the 2°C isotherm. The mean $\text{size}_{\text{assemblage5}}$

in the seasonally dynamic coastal upwelling zone is also smaller than expected from the global size-temperature trend (Fig. 3.4).

Test sizes of foraminiferal species have been previously documented to be smaller in frontal and upwelling areas (Ortiz et al. 1995). These environments are characterized by high turbulence along different water masses, frequently appearing eddies (Beckmann et al. 1987), and storm events (Schiebel et al. 1995), all of which lead to expatriation (Berger 1970; Weyl 1978) and vertical displacement of biota. Fronts appear to function as environmental barriers (Schiebel et al. in press) between three stable ecosystems, each harbouring groups of well-adapted species able to grow to large sizes. Frontal and upwelling areas may inhibit growth directly by their high environmental variability, but also indirectly by light attenuation, caused by high plankton standing stocks. The resulting lowered symbiotic activity of the few symbiont-bearing species living in these environments (Bijma et al. 1992; Ortiz et al. 1995) may also cause size reduction. At very high primary productivity rates characteristic for upwelling areas, a decrease in test sizes suggests that there is a global productivity optimum for foraminifers at primary productivity rates of about 150 g C $m^{-2}a^{-1}$. The smaller $size_{assemblage5}$ observed in upwelling assemblages is additionally influenced by the absence of many subtropical species which leads to a dominance of temperate *Globigerina bulloides*, a comparably small species.

Some species, such as *G. inflata* and *G. truncatulinoides* show several abundance optima with respect to global temperature variability (Prell et al. 1999). *G. inflata* has been considered a species with specific adaptation to frontal environments. Our analyses, however, demonstrate that two temperature-related optima in abundance and size exist, neither of which is at temperatures indicative for any front (Fig. 3.7). The increase in relative abundance may result primarily from the absence of other species. *G. truncatulinoides* is known to be a very deep-dwelling species (Hemleben et al. 1989) and might, therefore, be less affected by fronts.

3.5.3 Local influence of Primary Productivity

Within most of the biogeographic zones (subpolar, temperate, subtropical and tropical), size is linked to primary productivity (Tab. 3.2). This relation seems to be complex, with an apparent positive correlation in the subtropical zone and a negative in the subpolar, temperate and tropical zones. The limited number of samples within each individual zone, however, makes reliable analyses difficult. A larger and more detailed data base will be required to better characterize the potential effects of shifting abundances and sizes with respect to primary productivity optima and the interfering variability in frontal zones. The two effects may balance each other in different ways within the biogeographic zones.

3.6 CONCLUSIONS

1. On a global scale, planktic foraminifers, as a group, increase in size from the poles to the tropics. This pattern can be attributed to the co-variation of several temperature-related effects, such as metabolic efficiency, carbonate supersaturation, diversity, species-replacement, and intraspecific size variation.
2. The close global temperature correlation of maximum size and relative abundance of individual species defines environmental optima, beyond which decreases in both size and abundance can be expected.
3. The size increase with increasing temperature is not monotonous, rather, it shows two local minima, one at 2°C and the other around 17°C where polar and subtropical fronts are respectively found. Fronts represent major environmental perturbations, acting as biogeographic barriers for shallow dwelling planktic foraminifers. They lead to unfavourable conditions resulting in smaller sizes. A few persisting species, e.g. *G. inflata*, become dominant in these areas and show little size response to the environmental conditions.
4. Assemblages from upwelling areas also show smaller sizes. Here, additional impacting effects may include decreased numbers of symbiont-bearing species, leaving e.g. *Globigerina bulloides* to become dominant, and lower symbiont activity caused by turbidity.
5. On a regional scale, where temperature ranges are reduced, the secondary effect of primary productivity may become more important. A better understanding of these effects would require size spectra analysis of single species in many additional samples.

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CHAPTER 4*

REACTION OF PLANKTIC FORAMINIFERAL SIZE TO LATE QUATERNARY CLIMATE CHANGE

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ABSTRACT

In a previous study, the geographical size distribution of the entire Holocene foraminiferal assemblages was found to be related to global environmental gradients such as temperature, primary productivity and the environmental variability (Schmidt et al., subm.). The present study demonstrates that these correlations are also recognisable in the Late Quaternary assemblages at three locations in the South Atlantic on temporal and latitudinal scales. The size response to temporal paleoenvironmental changes during glacial-interglacial cycles in the late Quaternary mimics the geographic Holocene size variations. We have compared these size changes with the best available paleotemperature proxies. The amplitude of assemblage size variation is directly related to the amplitude of the Late Quaternary climatic fluctuations. More stable environments, such as the subtropical gyres, display the smaller size changes.

The documented changes in the assemblage size are caused by species replacement and intraspecific size variations. The relative importance of these processes depends on the environmental setting. Species reach their maximum size and abundance under optimum conditions and decrease in size if environmental conditions differ from this optimum. In low latitudes, the ecological tolerance of species is narrow and environmental variation induces species replacement. In high latitudes, species occupy broader niches, and hence temperature changes lead to a pronounced intraspecific size variation.

During the Late Quaternary, temperature variations caused latitudinal shifts of foraminiferal species distribution, and assemblage size changes along a north-south gradient. Variations in size can provide information about the ecological preferences of foraminiferal species, since a species reaches its maximum possible size at its ecological optimum. Our study shows that during this period, foraminiferal species were able to conserve stable ecological preferences, responding to the glacial-interglacial environmental changes by tracking a suitable habitat through geographical shift of their distribution.

Keywords

Planktic foraminifers, Quaternary, size, adaptation, paleoceanography

4.1. INTRODUCTION

Planktic foraminifers are free-floating marine protists that are widely distributed in the surface waters of the world's ocean. The excellent preservation, global occurrence and high abundance of planktic foraminifers within Cenozoic marine deep-sea sediments is one of the prime reasons for the extensive application in paleoceanographic and paleoclimatic studies. The analysis of species compositions (Imbrie and Kipp, 1971; Imbrie et al., 1973), stable isotopes (Shackleton and Opdyke, 1973; Hays et al., 1976), and other chemical tracers of foraminiferal tests, e.g. Mg/Ca (Elderfield and Ganssen, 2000), and Cd/Ca ratios (McCorkle et al., 1995), Boron isotopes (Sanyal et al., 1995) have proven to be valuable tools for paleoclimatic and paleoceanographic reconstructions. Morphological criteria considered in such studies have been size, shape and coiling direction of the test whose changes have been related to variation in temperature (Ericson, 1959; Bé et al., 1973; Hecht, 1976; Naidu and Malmgren, 1996) or fertility (Naidu and Malmgren, 1995).

The size of an organism varies with changing environmental conditions in both modern and fossil records (Peters, 1983; Skelton, 1993). Based on modern biogeographic size studies, microfossil size variation is used to reconstruct past environmental change, in both continental (LaBarbera, 1989; Dayan et al., 1991; Bown et al., 1994) and marine environments (Kennett, 1968; Bé and Duplessy, 1976; Malmgren and Kennett, 1978; Naidu and Malmgren, 1995). Studies of foraminifers in the Late Quaternary demonstrate size fluctuations in the vicinity of frontal systems or in upwelling-areas (Bé and Duplessy, 1976; Malmgren and Kennett, 1978; Naidu and Malmgren, 1995) and, in contrast in the central Caribbean, no size variations possibly due to stable environmental conditions (Malmgren and Healy-Williams (1978)).

These studies of paleoceanographic and –climatic change are all based on the assumption of an analogous environmental adaptation of the organisms, carrying the signal, in the past as in the present. Here we use the test size of entire planktic foraminiferal assemblages and species to analyse the effect of climate change on foraminiferal size, to define environmental preferences and to trace these back in time. The size spectrum of entire foraminiferal assemblages, estimated by the upper range of the distribution of maximum diameter measurements on each foraminifer of the assemblage, varied also according to environmental gradients in the Holocene. Temperature-related effects were identified as the cause for an increase in assemblage size from the poles to the tropics and environmental factors of secondary importance, such as primary productivity and environmental dynamics of frontal systems causing deviations from this trend.

This previous study was focused on biogeographic variations of size changes in Holocene faunas. To investigate the effect of temporal environmental variations, we concentrate in the present paper on the late Quaternary, which is characterised by large environmental variations, i.e. glacial- interglacial cycles. In response to these temporal environmental variations, size variations of planktic foraminiferal species are expected and environmental preferences can be traced. The present study of assemblage size variations in the Quaternary will allow us to test the following hypotheses.

1. Biogeographically, planktic foraminiferal assemblage size depends on temperature, primary productivity and environmental dynamics of frontal systems. We propose that temporal changes of these parameters related to the Quaternary climatic fluctuations would also cause size changes.
2. The climatic fluctuations display different amplitudes depending on the geographical setting. We expect that the size response is proportional to the extent of physical environmental change with large size variation in environments which have a strong glacial-interglacial contrast.
3. The variations in the physical environment can influence foraminiferal assemblage size through various biological processes, i.e. changes in the composition of the foraminiferal fauna, and intraspecific size variation. The relative importance of both processes has been addressed by comparing assemblage size variations on the one hand, to changes in the relative abundance of species typical of given environments, on the other hand, to intraspecific size changes of a given species, *Globorotalia truncatulinoides.*
4. Intraspecific size variations are related to ecological preferences of foraminiferal species. It has been shown in the Holocene study (Schmidt et al., subm) that a species reaches its maximal possible size in optimal ecological conditions. However, ecological preferences may change through time as an adaptive response to environmental change occurs. Therefore, by analysing the contribution of different species to the assemblage size variations, we tested whether their ecological preferences remained stable through the Late Quaternary.

To test these hypotheses, we focus our study of the foraminiferal size record on the last 300 kyrs using samples from three cores taken in different environmental settings in the South Atlantic: a) the equatorial upwelling - GeoB1105, b) the subtropical gyre - Geob1413 and c) the subpolar zone of the polar frontal system - PS2498 (Fig. 4.1).

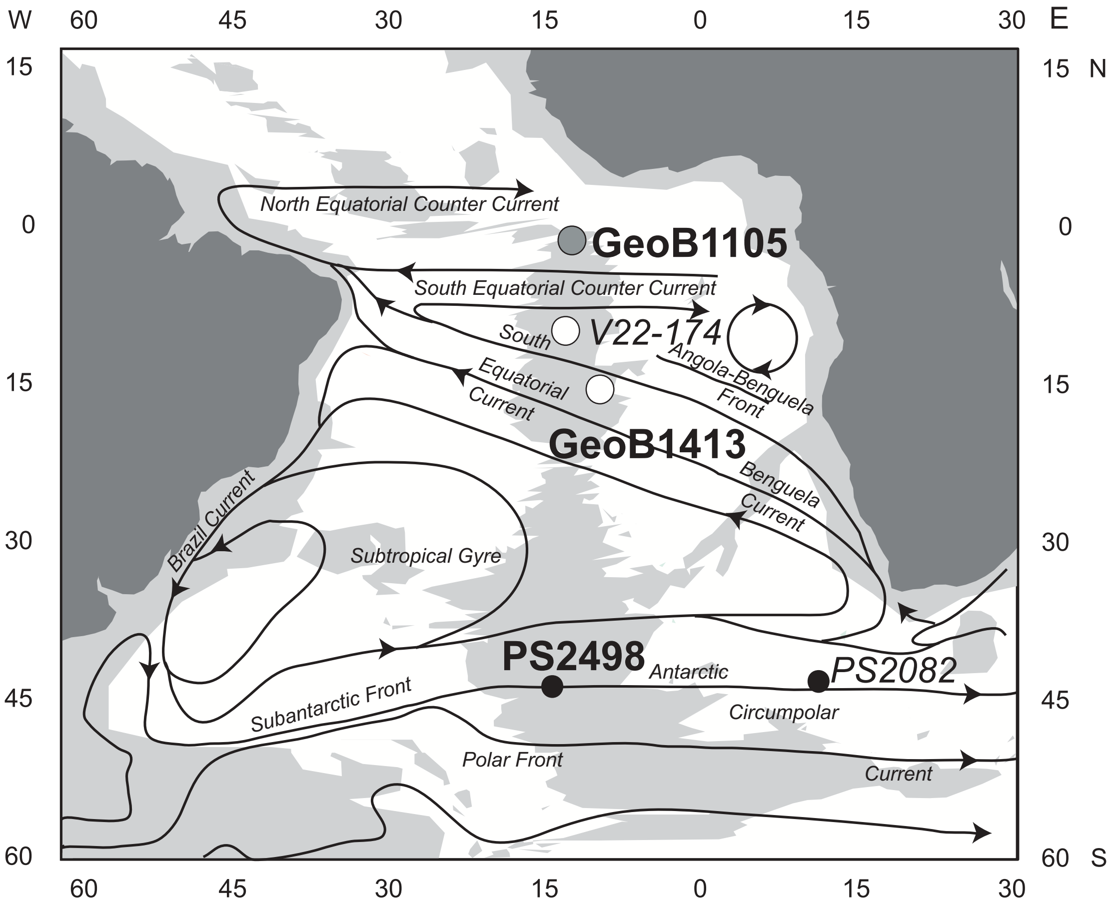

Figure 4.1: Core locations, main current systems and fronts in the South Atlantic. Currents after Peterson and Stramma (1991). Shaded area indicates depth less than 4000 meters. Bold labels indicate cores investigated for foraminiferal size data, italic labels cores with reference data.

4.2. ENVIRONMENTAL SETTING AND FAUNAL COMPOSITION

4.2.1. Modern environmental setting

The modern South Atlantic is dominated by a large subtropical gyre, which is bordered by the equatorial current system in the north, the subtropical front in the South, the Benguela Current in the east and the Brazil current in the west (Fig. 4.1). The three cores studied for size variation are located on the southern Mid-Atlantic Ridge well above the lysocline (Tab. 4.1). They represent a meridional transect, with core GeoB1105 in the equatorial upwelling zone, core GeoB1413 at the edge of the subtropical gyre and core PS2498 near the subantarctic front (Fig. 4.1). Age models, sedimentology and paleoceanography of these cores are discussed in detail by Wefer et al. (1996b), Meinecke (1992), Kemle-von Mücke (1994) and Mackensen et al. (2001).

Table 4.1: Core location, water depth, time interval investigated, average sedimentation rate and reference for the age models. Cores investigated for foraminiferal size are in bold, and cores with reference data in italic.

Label	Lat [°]	Long [°]	Depth [m]	Age [kyrs]	Average Sedimentation Rate [cm/kyrs]	
GeoB1105-4	1°39.9 S	12°25.7 W	3225	300	4.80	(Meinecke, 1992)
GeoB1413-4	15°40.8 S	9°27.3 W	3789	400	1.07	(Kemle-von Mücke, 1994)
V22-174	10°1S	12°52 W	2630		1.97	(Imbry et al., 1984)
PS2498-1	44°09.2 S	14°09.2 W	3783	130	8.94	(Mackensen, 2001)
PS2082	43°15 °S	11°45 °E	4610		3.55	(Mackensen et al., 1994)

Table 4.2: Environmental characteristics for the site locations of studied cores. Temperature values represent the annual average sea surface temperature (SST in °C), seasonal temperature difference (δTs), glacial/interglacial temperature difference (δTgl) and the depth of thermocline in meter (Δ of T). Additionally the primary productivity (PP), and main components of the fauna are given. Modern values for temperature (Levitus et al., 1994) and primary productivity (Antoine et al., 1996). References for proxies and faunal composition see table 4.3.

Core	SST [°C]	δTs [°C]	δTgl [°C]	Δ of T [°C]	PP [$gCm^{-2}a^{-1}$]	Fauna
GeoB1105	25.9	4.5	4-5 summer 7-8 winter	20 to 30 summer 75 winter	100	*G. ruber* (w & p), *G. sacculifer,* *G. menardii, G. siphonifera,* *G. glutinata, G. inflata,* *G. bulloides, G. calida*
GeoB1413	23.2	2.5	7-8		45 - 60	*G. ruber, G. sacculifer*
PS2498	9.7	3.0	7	< 50 m	60	*G. bulloides* *N. pachyderma (d & s)* *G. inflata*

The equatorial upwelling core, GeoB1105, is from a location which is today characterised by strong seasonal upwelling leading to an annual temperature range of 4.5°C (Levitus et al., 1994), strong seasonal variations in the depth of thermocline (Wolff et al., 1999), and high primary productivity (Berger, 1989). Rather stable environmental conditions, a deep thermocline and low primary productivity are typical for the subtropical gyre, from where core GeoB1413 was secured. The seasonal variability at GeoB1413 is less than 2.5°C. The subpolar environment, corresponding to the location of core PS2498, is characterised by lower temperatures, seasonal variability, a shallow thermocline and an intermediate primary productivity (Tab. 4.2).

4.2.2. Holocene versus Late Quaternary

Glacial paleotemperatures were colder at the locations of all three investigated cores. In the equatorial upwelling region (GeoB1105), glacial paleotemperatures are calculated to have been 4-5°C colder during summer and 7-8°C colder during winter (Meinecke, 1992). This indicates an increase in seasonality at this core during glacial periods. In the subtropical gyre (GeoB1413), a temperature decrease of 2.5°C at Termination I was determined (Mulitza, pers. com. 2001). In the subpolar environment (PS2498), the temperature difference between the Holocene and the last glacial maximum is estimated to have been 7°C (Brathauer and Abelmann, 1999).

Strong seasonal contrast during glacials at the equatorial upwelling site GeoB1105 suggests intensification of the seasonal upwelling, which is supported by the total organic carbon content of the sediments (Schneider et al., 1996). At this site, the paleoproductivity estimates were higher in glacials with values around 160 g C $m^{-2}a^{-1}$, compared to 40 g C m^{-2} a^{-1} as the minimum in interglacials 5 and 7 (based on unpublished data of Peter Müller, see http://www.pangaea.de for data following the method described in Stein, 1991). For GeoB1413, no primary productivity reconstructions are available. However, the carbon isotopic composition of planktic foraminifers points to a nutrient depletion of thermocline water during glacial times (Wefer et al., 1996a). Primary productivity at PS2498, based on the concentrations of organic material in the sediments (Mackensen et al., 2001) and calculated with the method of Müller and Suess (1979) and Stein (1991), varies from 61 gC m^{-2} a^{-1} during interglacial up to 110 gC m^{-2} a^{-1} during the last glacial maximum indicating the northward shift of the polar front during glacials (Mackensen et al., 2001).

The different environmental conditions result in distinct faunal compositions throughout the Late Quaternary in the cores. The equatorial upwelling fauna of GeoB1105 displays a mixing of tropical species, such as *Globigerinoides ruber* (white and pink), *Globigerinoides sacculifer*, *Globorotalia menardii*, and species associated with upwelling, such as *Globorotalia inflata*, *Globigerina bulloides*, and *Globigerinella calida* (Meinecke, 1992). The subtropical gyre assemblage of core GeoB1413 is mainly composed of *G. ruber* with minor contribution of *G. sacculifer* (Kemle-von Mücke, 1994). The subpolar fauna of core PS2498 is dominated by *G. bulloides* and with a minor proportion of *Neogloboquadrina pachyderma* (dextral and sinistral) and *G. inflata* (Niebler and Gersonde, 1998). All species contributing to the Holocene assemblages, except *G. menardii*, are also present during glacials, although relative abundances vary.

4.3. MATERIAL AND METHODS

4.3.1. Material

Three deep-sea cores from the South Atlantic were used in this study. All three cores were located at water depths above present lysocline (Broecker and Takahashi, 1978). They contain undisturbed sediments and well-calibrated age models based on oxygen isotope measurements (Meinecke, 1992; Kemle-von Mücke, 1994; Mackensen et al., 2001). Very different sedimentation rates result in variable age coverage in the three cores (Tab. 4.1): i.e., 300 kyrs for GeoB1105, 400 kyrs for GeoB1413, and 130 kyrs for PS2498. Samples for assemblage size investigations have been taken at intervals representing on average every 3.2 kyrs for GeoB1105 (98 samples), 4.7 kyrs for GeoB1413 (81 samples), and 2.3 kyrs PS2498 (56 samples). Samples for the intraspecific size variability were selected to represent the last 130 kyrs.

Foraminifers are well preserved in the two northernmost cores GeoB1105 and GeoB1413 (Meinecke, 1992). In PS2498 a high proportion of siliceous microfossils, especially the glacial intervals, could reflect carbonate dissolution, although the occurrence of *G. bulloides* indicates a good fossil preservation, since this species is solution susceptible (Berger, 1968). The foraminifers were analysed in the fraction >150µm to allow comparison with the faunal composition data from Meinecke, (1992) and Mix et al. (1999). Additionally, this size fraction allows one to exclude juvenile forms and focus on the adult stage within the ontogeny of the foraminifers.

4.3.2. Size analysis

In the present study, three different types of size proxies are considered: (1) an estimator of the size distribution within the entire assemblage, (2) the maximum size reached per species and (3) the average size of a given species, *Globorotalia truncatulinoides*.

Assemblage size

For the entire assemblage size measurement, a complete split of each sample was analysed, which, on average, contained 2012 individuals (min. 779, max. 4414). The entire dataset contains 462.961 measurements. Using an automated image analysis system (Bollmann et al., subm.), the maximum diameter of each unoriented foraminifer was measured, since this size parameter is least affected by orientation. Because the minimum diameter is given by the sieve size (>150µm), it represents an artificial cut-off of the natural size distribution and, therefore, does not have any biological significance. Since the distributions are highly skewed towards larger sizes, the most suitable descriptor of the distribution is the value separating the largest five percent of the distribution from the smallest 95% ($\text{size}_{\text{assemblage5}}$). Details of the measuring technique and the choice of descriptors to characterise the assemblage are given in Schmidt et al. (subm.).

Maximum size per species

Investigating variations in the maximum size reached by foraminiferal species can provide insight into their ecological preferences. In this purpose, the largest size reached per species was estimated by considering the largest 40 specimens of the assemblage, identifying the species present, and determining the maximum size they reached. This procedure was applied for three glacial and interglacial stages.

Average size of Globorotalia truncatulinoides

To test the impact of environmental change at the scale of a species, the size variability of *G. truncatulinoides* was analysed. This taxon was selected because it is present in all cores throughout the investigated time span. Its abundance in the total foraminiferal assemblage ranges between 0.1 and of 6% of the fauna, allowing its study in all the samples without contributing strongly to the assemblage size changes. All specimens in a split of the fraction >150 µm, on average 40 specimens (min. 8, max. 76), were picked and oriented. The maximum diameter measured for the spiral side was chosen as size estimator ($\text{size}_{\text{trunc}}$), because it is the most comparable to the unoriented size measurements used in for the other size estimators (assemblage size and maximum size per species).

4.3.3. Environmental proxies

The discussion of climate and climatic change in the more remote past depends on “proxy” evidence. Proxies are measurable characteristics of sediments, which, via transfer functions, can be used to describe environmental parameters. Several paleo-proxies are available to describe the environmental change between glacial and interglacial periods and to interpret the observed foraminiferal assemblage size change (Tab. 4.3). These are oxygen and carbon isotopes of various planktic and benthic foraminifers, temperature and primary productivity reconstructions, and estimators of species richness.

Table 4.3: Overview of paleoenvironmental proxies considered in the present study. Paleotemperature estimates are based on changes in the composition of radiolarian or foraminiferal faunas (Imbrie and Kipp, 1971; Meinecke, 1992; Brathauer and Abelmann, 1999) or on alkenone measurements (Schneider et al., 1996). The mass accumulation of total organic carbon in the sediments (Corg), density and porosity have been used to calculate paleoproductivity.

Label	Proxy	Reference
GeoB1105	Carbon/Oxygen isotopes of *G. ruber, G. inflata, G. crassaformis,*	(Meinecke, 1992)
	Carbon/Oxygen isotopes of *F. wuellerstorfi*	(Bickert, 1992)
	Species richness	(Meinecke, 1992)
	Diversity	(Meinecke, 1992)
	temperature reconstruction (forams)	(Meinecke, 1992)
	alkenone temperature	(Schneider et al., 1996)
	Corg, density, porosity	(Meinecke, 1992; Müller, unpub. data)
GeoB1413	Carbon/Oxygen isotopes for *G. ruber, G. crassaformis*	(Kemle von Mücke, 1994)
V22-174	SST reconstruction	(Imbrie et al., 1989)
	Species richness	(Mix et al., 1999)
PS2498	Carbon/Oxygen isotopes of *F. wuellerstorfi*	(Mackensen et al., 2001)
	Primary productivity	(Mackensen et al., 2001)
PS2082	Temperature (radiolaria)	(Brathauer and Abelmann, 1999)

For core GeoB1105, several proxies, e.g. the isotopic composition of benthic and planktic carbonate, paleotemperature (based on foraminiferal transfer functions and modern analogue technique) and paleoproductivity calculation, and faunal composition were determined (Tab. 4.3). For core GeoB1413 the isotopic composition of planktic foraminiferal shells are available. Equivalent age (Imbrie et al., 1984) faunal composition (Mix et al., 1999) and paleo- temperature data (Imbrie et al., 1989), based on foraminiferal assemblages, were taken from core V22-174, which was taken at a location between that of cores GeoB1105 and GeoB1413 (Fig. 4.1). The benthic isotope data and primary productivity reconstructions were accessible at PS2498. Paleotemperatures, based on radiolaria, were used from core PS2082 (Brathauer and Abelmann, 1999), which was taken at the same latitude, but 25° east of core PS2498 (Fig. 4.1).

Measurements of $\delta^{18}0$ and $\delta^{13}C$ values were previously performed on the benthic foraminifer *F. wuellerstorfi* in GeoB1105 (Bickert, 1992) and PS2498 (Mackensen et al., 2001), and on the planktic species *G. ruber* (GeoB1105, Meinecke, 1992; GeoB1413, Kemle von Mücke, 1994), *G.crassaformis* (GeoB1105, Meinecke, 1992; GeoB1413, Kemle von Mücke, 1994) and *G. inflata* (GeoB1105, Meinecke, 1992). In planktic foraminifers, changes in oxygen isotope values represent fluctuations in the ice volume and the local temperature. A positive shift of the $\delta^{18}0$ values indicates a cooling event and/or an increase in polar ice volume. Changes in $\delta^{13}C$ values of planktic foraminifers are a result of variations in surface water primary productivity. In the case of benthic foraminifers, changes in $\delta^{13}C$ values are related to degradation of organic matter at the sea floor. An increase in the primary productivity shifts the $\delta^{13}C$ values of planktic foraminifers towards more positive values, due to the preferential fixation of ^{12}C during photosynthesis. Such an increase in productivity will cause enhanced export of organic material to the sea floor and degradation of organic matter which consequently leads to more negative $\delta^{13}C$ values of benthic foraminifers. Paleoproductivity estimates (Müller and Suess, 1979; Stein, 1991) were derived from changes in the total organic carbon contents of sediments. The reconstruction is based on the assumption that an increased primary productivity at the sea surface will enrich the sediment in organic matter. Paleotemperature estimates are based on changes in the composition of radiolarian or foraminiferal faunas (Imbrie and Kipp, 1971; Meinecke, 1992; Brathauer and Abelmann, 1999). Based on the foraminiferal faunal counts, we determined species richness and ratios between groups with specific environmental adaptations, symbiont bearing versus the non- symbiont bearing foraminifers and tropical versus upwelling species.

4.3.4. Statistical analysis

The relationship of $size_{assemblage5}$ and $size_{trunc}$ with environmental proxies was tested using a simple linear regression. The difference between glacial and interglacial measurements was examined with an analysis of variance (ANOVA).

4.4. RESULTS AND INTERPRETATION

4.4.1. Geographic and temporal size-temperature correlation

Throughout the Late Quaternary, the $size_{assemblage5}$ does not increase latitudinally from the subpolar to the tropical environment, but according to increasing sea surface temperature (Fig. 4.2). The smallest $size_{assemblage5}$ (300-492µm) is found in the subpolar core PS2498, the largest size (472-568µm) in the subtropical gyre core GeoB1413 and the intermediate size (378-527µm) in the equatorial core GeoB1105 (Fig. 4.2). Our results are therefore in good agreement with the general size-temperature relationship emerging from the Holocene study (Fig. 4.3).

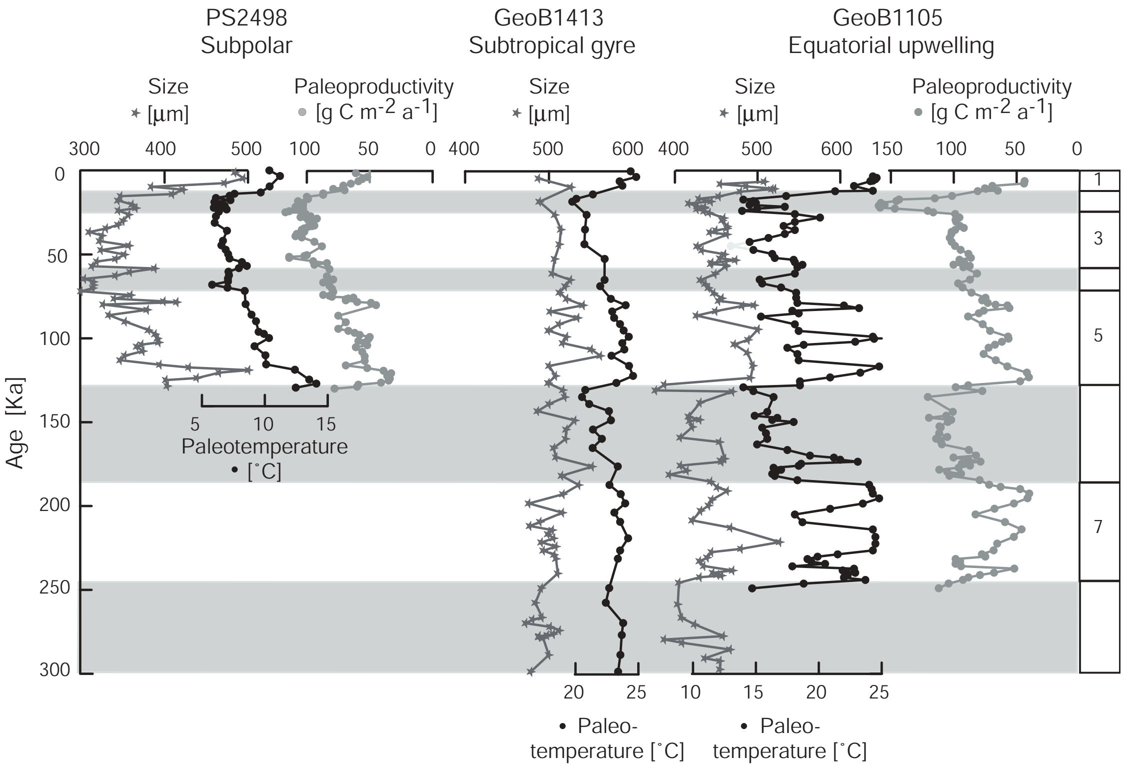

Figure 4.2: Plot of size$_{\text{assemblage5}}$ changes compared to paleotemperature (data from Brathauer and Abelmann, 1999; Imbrie et al., 1989; Meinecke, 1992) and paleoproductivity (Mackensen et al., 2001; Meinecke, 1992, Müller, unpub. data) for the last 300 kyrs at the three locations. Numbers represent the isotope stages, and grey bars indicate glacial stages.

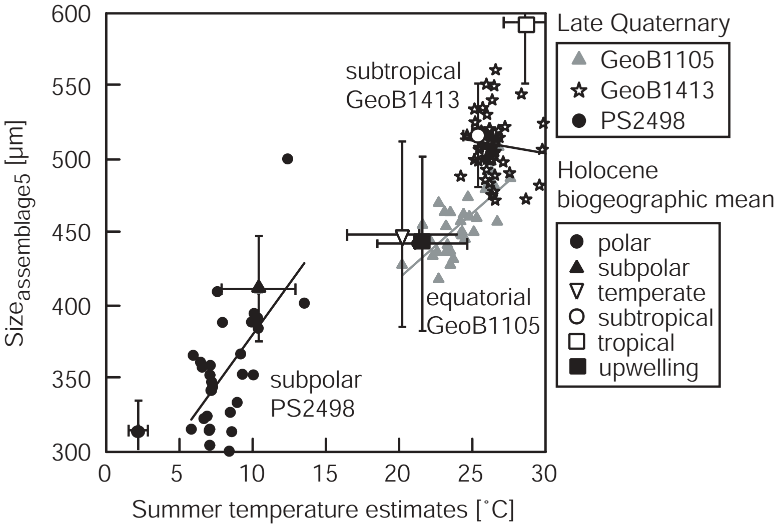

Figure 4.3: Size$_{\text{assemblage5}}$ (µm) compared to paleotemperature (°C) of all samples with paleo-temperature estimates (for references see Fig. 4.2). Lines represent significant linear correlation for each core. Regression coefficients see Table 4. Additionally, the mean size$_{\text{assemblage5}}$ per biogeographic zone of the Holocene are indicated (Schmidt et al., subm). Error bars indicate the standard deviation for temperature, respectively size$_{\text{assemblage5}}$.

Variation in size does not only occur geographically in the Late Quaternary, but also temporally. The variations of size$_{\text{assemblage5}}$ through each core can be related to the changes in temperature (Tab. 4.4). The largest temporal size range is observed in core PS2498, which is related to a temperature variation of 7°C. Core GeoB1105 is also characterised by large size variations in accord with paleotemperature range of 12°C during the last 300 kyrs. Little size change is found in core GeoB1413 during the last 300 kyrs with an associated temperature change of 5°C.

Table 4.4: Linear correlation of environmental factors with size$_{\text{assemblage5}}$ for all cores. Values indicated are correlation coefficients (r). Bold values indicate significant correlation ($p < 0.05$); values in italic in "all" are based on only two cores (SST cold for GeoB1105 and GeoB1413, primary productivity for GeoB1105 and PS2498). For references see Tab. 4.2. Abbreviations MAT = Modern analogue technique and TF = transfer functions refer to paleotemperature estimates based on faunal composition (see Meinecke, 1992 for explanation), S = species richness

	Proxy	All	GeoB1105	GeoB1413	PS2498
oceanography	$\delta^{18}O$ *wuellerstorfi*		0.577		0.741
	$\delta^{13}C$ *wuellerstorfi*		0.55		
	$\delta^{18}O$ *ruber*		-0.552	-0.205	
	$\delta^{13}C$ *ruber*		0.359	0.114	
	$\delta^{18}O$ *inflata*		-0.186		
	$\delta^{13}C$ *inflata*		-0.142		
	$\delta^{18}O$ *crassaformis*		-0.134	0.101	
	$\delta^{13}C$ *crassaformis*		-0.399	-0.18	
temperature	SST warm MAT		0.716		
	SST cold MAT		0.798		
	SST warm TF		0.446	-0.163	
	SST cold TF		0.655	0.017	
	SST warm	0.909			
	SST cold	0.802			
	SST radiolaria				0.629
	SST alkenone		0.622		
productivity	primary productivity	-0.049	-0.641		-0.582
diversity	S		0.608	0.092	

Linear regression (Tab. 4.4) indicates a positive correlation of size and temperature on a global scale, when all three cores are considered together. A similar relationship emerges at a local scale in the subpolar and the equatorial upwelling samples (Fig. 4.3). No significant correlation between size and paleotemperature is found for core GeoB1413 in the subtropics, probably as a consequence of reduced size and temperature changes. Therefore, both, the geographical and temporal size variation in the Quaternary are congruent with the biogeographic size variations (Fig. 4.3), as observed for the Holocene (Schmidt et al., subm.).

4.4.2. Assemblage size changes and paleo-productivity

In Holocene assemblages, negative deviations from the general size-temperature relationship were related to primary productivity variation and the influence of frontal systems (Schmidt et al., subm). In the Late Quaternary, negative significant correlation of paleoproductivity and size$_{\text{assemblage5}}$ is observed at a local scale within the subpolar (PS2498) and equatorial upwelling (GeoB1105) areas (Fig. 4.2), although no overall size-paleoproductivity correlation could be found (Tab. 4.4). This is consistent with the results of the Holocene study (Schmidt et al., subm.), where on a regional scale productivity influences size$_{\text{assemblage5}}$, whereas on a global scale temperature emerges as the main factor causing size$_{\text{assemblage5}}$variations.

However, effects of productivity on size seem to be different according to the local setting, since the slope of the size-productivity relationships at PS2498 and GeoB1105 are different (Fig. 4.4).

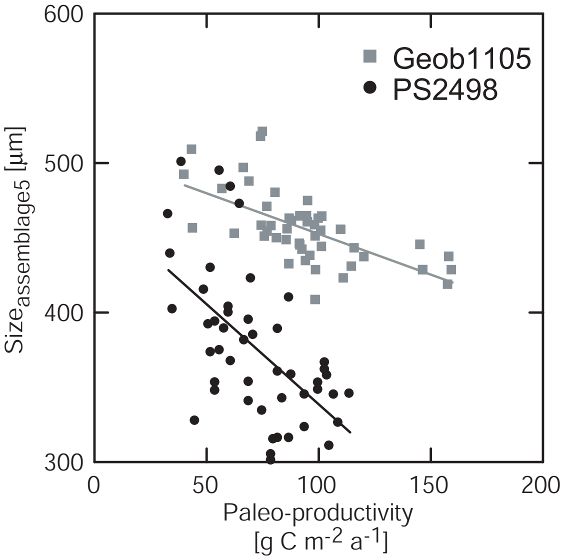

Figure 4.4: Plot of paleoproductivity (g C m^{-2}a^{-1}) versus size$_{\text{assemblage5}}$ (µm) for core GeoB1105 (grey circles) and core PS2498 (black circles). Primary productivity estimates for PS2498 from Mackensen et al. (2001), and for GeoB1105 based on data from Müller (unpublished data) and Meinecke (1992). Regression coefficients see Table 4.4.

4.4.3. Assemblage size changes and species composition

Changes in temperature, productivity and frontal dynamics can affect size$_{\text{assemblage5}}$ through different processes. First, the environment can influence the size of foraminifer species. Second, they can affect the size$_{\text{assemblage5}}$ by changing the faunal composition of the assemblage.

We tested the effect of species replacement for the equatorial upwelling core GeoB1105, where a strengthening of the upwelling during glacials has been previously documented (Wefer et al., 1996a). Species replacement occurs within this core according to the intensity of the upwelling situation (Meinecke, 1992), since an equatorial upwelling assemblage consists of different species than those found in a tropical assemblage. Assemblage size covaries at GeoB1105 with the ratio of tropical vs. upwelling species (Fig. 4.5), and the observed size range covered in core GeoB1105 (378-527µm) corresponds to the size difference observed in the Holocene between upwelling assemblages (451µm) and subtropical/tropical assemblages (509/625) (Schmidt et al., subm).

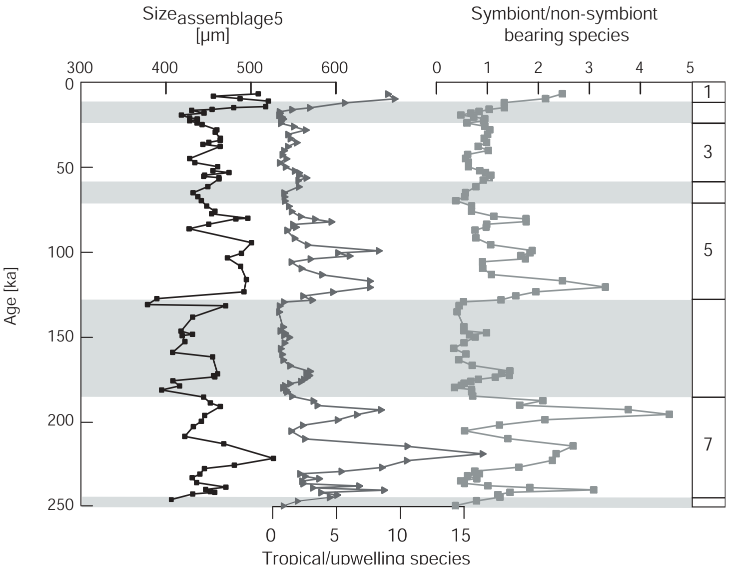

Figure 4.5: Plot of size$_{assemblage5}$ (µm) (black squares) versus ratio of tropical to upwelling species (black triangles) and symbionts bearing to non-symbiont bearing species (grey square) in core GeoB1105. Ratios based on data from Meinecke (1992).

4.4.4. Size changes within species: indicator of optimum ecological conditions

Changes in environmental conditions affect not only the species composition, but they can also cause intraspecific size change. Previous studies (Hecht, 1976; Schmidt et al., subm) have shown that foraminifer can grow larger when being in optimum ecological conditions, whereas small size results from unfavourable environments. Species with a global occurrence, such as *Globorotalia truncatulinoides*, *G. inflata*, and *G. crassaformis*, show an increase in size towards the tropics, a pattern very similar to the one observed in the Holocene (Fig. 4.6a).

In contrast, the maximum sizes found for *Globigerinoides sacculifer*, *G. menardii* and *G. tumida* in the Late Quaternary study are much smaller than those determined for the Holocene (Fig. 4.6b). This difference may be due to the fact that the temperature range covered in the present study is too limited and do not include the optimum temperature conditions of these species. In the Holocene, these species display their optimum temperature above 27°C, whereas the warmest paleotemperature estimates in the present study are 26.4°C.

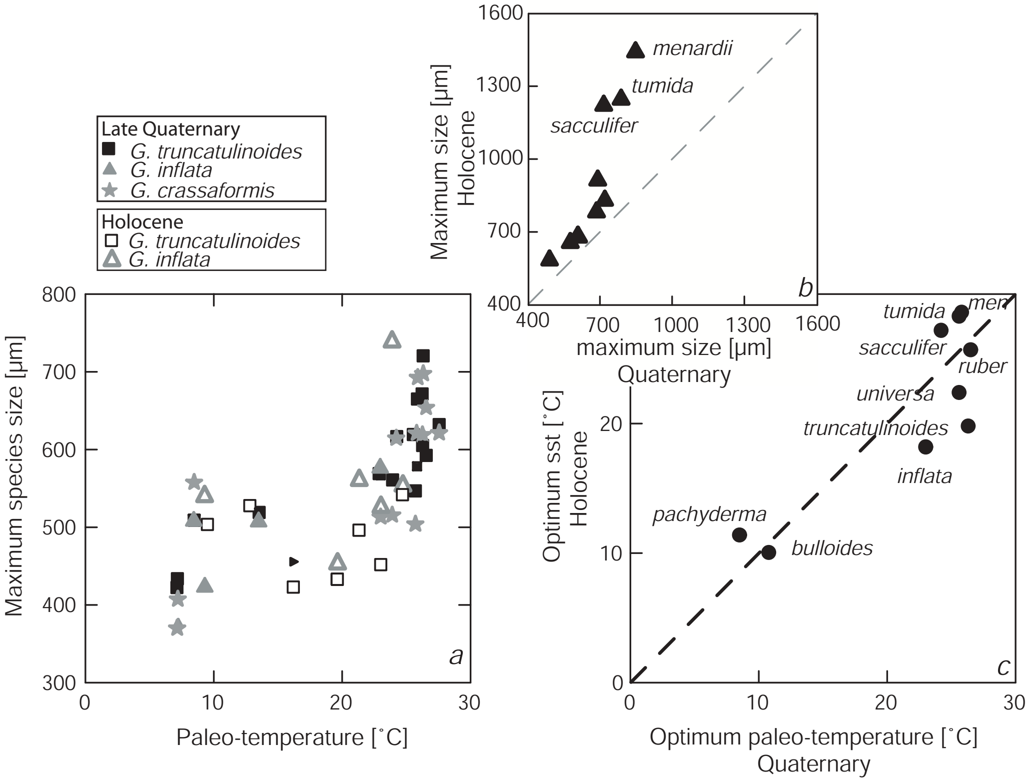

Figure 4.6: a) Maximum size (µm) for *G. truncatulinoides*, *G. inflata*, *G. crassaformis* (open symbols Holocene geographic data (Schmidt et al., subm.); filled symbols Late Quaternary based on isotope stages 2 to 8) vs. paleotemperature, b) Maximum sizes for investigated species in the Holocene compared to maximum sizes in the Late Quaternary. Line indicates 1:1 relationship. c) Optimum sea surface temperature (°C) in the Holocene vs. optimum (paleo) temperatures in Late Quaternary (isotope stages 2 to 8) for the investigated species. Ecological optimum is estimated as the temperature where each species reaches its largest size and maximum abundance (for references of temperature estimates see Fig. 4.2). To gain consistency within the temperature estimates from all three sites, optimum paleotemperatures are summer estimates, in contrast to winter estimates in Figure 2. Line indicates 1:1 relationship.

To compare the Late Quaternary results with the Holocene, we plotted the observed optimum temperature of the investigated species in the Holocene vs. the Quaternary, (Fig. 4.6c). A good general agreement exists between the two ranges of estimates, suggesting stability in the ecological preferences in temperature of the investigated species over the Late Quaternary (stages 2 to 8).

To increase our understanding of the influence of the intraspecific variation on size$_{\text{assemblage5}}$, we studied in detail the reaction of *G. truncatulinoides* to the environmental change in the last 130 kyrs. This species was chosen because it is present in all cores in sufficient number for statistical analysis. Although *G. truncatulinoides* contributes to the size$_{\text{assemblage5}}$, it never dominates the largest fraction, because several other species constitute to the largest five percent of the assemblage. In all the cores considered, *G. truncatulinoides* shows significant size variability during the last 130 kyrs (Fig. 4.7) although the difference between glacials and interglacial is not statistically significant in cores PS2498 and GeoB1413 (ANOVA: p=0.576, p = 0.422 respectively). In core GeoB1105, size$_{trunc}$ shows differences between glacials and interglacials, but the significance is low (r^2 = 0.198, p= 0.020). In none of the cores size$_{trunc}$ is significantly correlated to size$_{assemblage5}$ (linear correlation GeoB1105: r^2 = 0.372, p = 0.061; GeoB1413: r^2 = 0.034, p = 0.359; PS2498: r^2 = 0.004, p = 0.807).

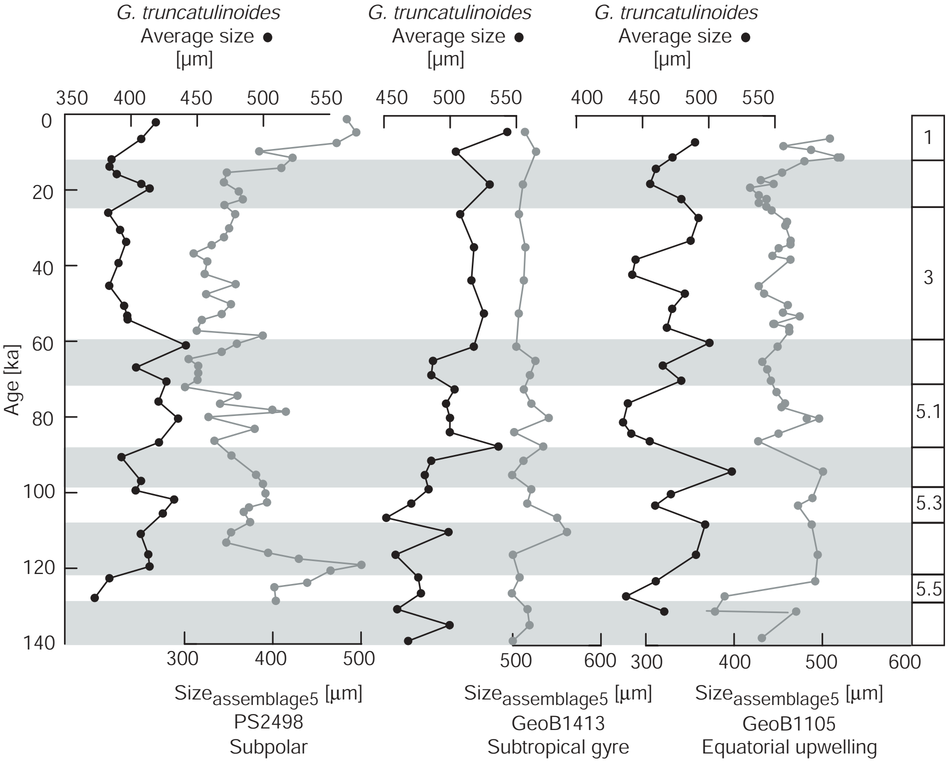

Figure 4.7: Size$_{assemblage5}$ (µm) and size$_{trunc}$ (µm) versus time for the last 130 kyrs in PS2498, GeoB1413 and GeoB1105. Shaded area represents glacial stages.

4.5. DISCUSSION

4.5.1. Influence of the physico-chemical environment on size

The relationship of $\mathrm{size}_{\mathrm{assemblage5}}$ of foraminifers with temperature, productivity and frontal dynamics defined in the Holocene (Schmidt et al., subm) persists during the last 300kyrs. As in the Holocene, the main trend emerging both at a global and a local scale is a size-temperature trend. However, locally, i.e. through one core, secondary factors, such as primary productivity and the environmental variability, become important.

Temperature-related effects are the main driving forces causing a $\mathrm{size}_{\mathrm{assemblage5}}$ increase towards the tropics and during the warm intervals of the late Quaternary.

Warm temperatures may lead to larger foraminiferal size due to several processes, such as higher metabolic rates of the organism (Caron et al., 1987a; Caron et al., 1987b; Bijma et al., 1990; Spero et al., 1991), increased carbonate supersaturation facilitating growth (Lea et al., 1999), and changes in species composition including higher diversity (see Schmidt et al., subm. for review).

Frontal systems and upwelling areas have been shown to interfere with these temperature-related effects in the Holocene (Schmidt et al. subm) and locally reduce size. Our results corroborate this observation. Frontal systems represent highly variable ecosystems unfavourable to most species adapted to more stable water masses. Therefore, none develop to this maximum possible size in these areas, causing a decrease in assemblage size (Schmidt et al., subm.).

Additionally, frontal systems and upwelling areas are regions of increased primary productivity. A relationship between size and primary productivity was already documented for several species (Naidu and Malmgren, 1995). Our results also indicate an influence of paleo-productivity. However, this factor co-varies at a global scale with both temperature and frontal dynamics, and their respective effects are therefore difficult to disentangle. In the environment characteristic for core GeoB1105 and core PS2498, a weak upwelling, respectively a larger distance from the front, results in low primary productivity, warm temperatures and low seasonal contrasts. Hence, the relationship of primary productivity and size may be related to the distance from the front, that is intensity of upwelling rather than to nutrient conditions per se.

4.5.2. Species replacement and intraspecific size variability

Varying abiotic environmental conditions cause changes in the faunal composition and intraspecific size variations which may, in turn, contribute to assemblage size differences. Species replacement influences $\text{size}_{\text{assemblage5}}$, because different species have different size spectra (Hecht, 1976). Upwelling zones appear to be unfavourable to tropical species and many subtropical to tropical species are absent, leading to a dominance of the temperate *Globigerina bulloides*. This species has a small size compared to most subtropical and tropical species (Hecht, 1976). Its dominance in upwelling assemblages will, consequently, results in a smaller $\text{size}_{\text{assemblage5}}$ being associated with a strengthening of upwelling compared to assemblage size occurring in tropical conditions.

Additionally, foraminiferal species can experience a decrease in test size in upwelling zones, which will enhance the decrease in assemblage size related to species replacement. Test sizes of foraminiferal species have been previously documented to be smaller in frontal and upwelling areas (Ortiz et al., 1995, Schmidt et al., subm). Foraminifer growth may be inhibited in these conditions because of high environmental variability, but also by light attenuation caused by high plankton standing stocks. Light is necessary to growth of symbiont-bearing species, which have been proven to reach larger test size compared to non-symbiont bearing species (Hecht, 1976). At high primary productivity conditions, light attenuation limits symbiont activity and consequently growth of symbiont bearing planktic foraminifers (Bé et al., 1981); additionally, it induces a species replacement of symbiont-bearing by non-symbiont bearing species.

Hence, similar processes influence the ratio of symbiont- versus non-symbiont-bearing species and the ratio of tropical to upwelling species. In agreement, we found at GeoB1105 a covariation of these ratios, both related to assemblage size variations (Fig. 4.5). This result underlines that a single abiotic cause, i.e. variation of strengthening of upwelling during glacials, results in variations of assemblage size due to the combination of several biotic response, i.e. species replacement of typically tropical by upwelling species, and non-symbiont by symbiont species.

Species replacement characterises biogeographic areas (Bé and Tolderlund, 1971) and leads to different assemblage sizes in different biogeographic zones (Schmidt et al., subm). This effect can largely explain the difference observed in the Late Quaternary record between each of the studied cores. Locally, variations in the upwelling intensity induced species replacement leads to temporal size variation in the equatorial core GeoB1105 (Fig. 4.5). During intensive glacial upwelling the proportion of symbiont-bearing species decreases to 20% from 60% in interglacial, causing a decrease in $\text{size}_{\text{assemblage5}}$. In contrast, in the subtropical gyre, the same species dominate cold and warm intervals in the record. Assemblage size variations in these cores, therefore, are not the result of species replacement and may be by intraspecific size variation.

In order to investigate the possible influence of intraspecific size change, we analysed the size variability of *G. truncatulinoides*. An overall geographic signal emerges, with larger size at higher temperature (Fig. 4.7); however, this analysis failed to reveal any fine-scale relationship of $\text{size}_{\text{trunc}}$ with environmental variations through time (Fig. 4.7). This absence of correlation could be explained by different hypotheses. First, *G. truncatulinoides* lives in deep waters down to 2000 meters (Hemleben et al., 1989). Therefore, proxies estimating sea-surface conditions may be unsuitable to describe *G. truncatulinoides* ecological preferences which could be related the depth of the thermocline (Lohmann and Schweitzer, 1990). Second, genetic analyses by de Vargas et al. (2001) indicate that *G. truncatulinoides* consists of four different genetic species, supposedly characterised by different ecological preferences, since three of the genetic species have been found segregated along a temperature gradient. Species replacement is therefore likely to occur. Hence, the down core $\text{size}_{\text{trunc}}$ measurements may be a combined result of species replacement within the *G. truncatulinoides* complex of species, and intraspecific size variation.

4.5.3. Differential response to environmental change of various amplitudes

Our results show that the relative importance of species replacement and intraspecific size changes depends on the environmental setting considered. Warm water species have narrow ecological tolerance, resulting in optima close from each other along a temperature gradient (Fig. 4.6c). Hence, an environmental change of limited amplitude will lead to species replacement. In comparison, few species are adapted to cold water, limiting the role of species replacement. Having wider environmental tolerance, these species can experience a large range of temperature and are therefore prone to display intraspecific size variations.

These schematic hypotheses can be tested in details, considering the mechanisms involved in the assemblage size variations through the different cores.

GeoB1105 – species replacement in equatorial upwelling systems

Temperatures are lower and primary productivity is higher during the glacial and interstadial phases (Wefer et al., 1996a) at this site. These changes are related to a strengthening of the African monsoon system during glacial intervals, which increases the upwelling in the equatorial Atlantic (Wefer et al., 1996a). The summer paleotemperature throughout the entire core ranges from 18 to 27°C. Several tropical and subtropical species have their optimum in this temperature range. Most of these species show such a strong decrease in size when moving out their optimum temperature that they don't contribute anymore to the largest 5% of the assemblage, considered in the present study as estimator of the assemblage size. Influence of intraspecific size variation on our estimation of assemblage size is therefore limited. In contrast, species replacement plays an important role since during cold phases, upwelling-species, e.g. *N. dutertrei*, *G. bulloides,* and *N. pachyderma* dominate the assemblage composition, whereas, in the warm intervals tropical species, e.g., G. *sacculifer*, *G. ruber*, *G. menardii,* are more frequent (Fig. 4.5). In cold intervals with vigorous upwelling and decreased temperatures, large tropical non-symbiont bearing species, such as *G. menardii*, disappear. Therefore, a decrease of the number of symbiont-bearing species, tropical species and a size decrease of the persisting symbiont-bearing species all contribute to smaller size during cold intervals.

GeoB1413 - environmental and size stability in the central gyre

The position of this core in the northern part of the subtropical gyre suggests stable environments as indicated by the limited variation in sea surface temperature and assemblage composition. Accordingly, changes in temperature is this core are less than in the other ones. $\text{Size}_{\text{assemblage5}}$ shows little variation through time, since limited the environmental variations do not induce neither species replacement, the assemblage composition in this environment being almost invariable (Mix et al., 1999), nor intraspecific size variations because the species present remain all the time close to their optimum.

PS2498 – subpolar frontal dynamics and intraspecific size variation

During glacial conditions, the polar front, which is situated today around 6° south of the location of core PS2498 (Peterson and Whitworth, 1989), moved northward and approached the location of the core. Consequently, during glacials, temperatures decreased, primary productivity increased and frontal dynamics increased. $\text{Size}_{\text{assemblage5}}$ closely responds to these variations. The largest species in the assemblage, in both warm and cold intervals, are *G. bulloides, G. truncatulinoides* and *N. pachyderma*, showing that the role of species replacement is limited. Intraspecific size variations seem to be more important. With a decrease in temperatures relative to Holocene values, these species are growing under conditions out of their optimum, and their size decreases (Schmidt et al., subm).

4.6. CONCLUSIONS

Based on a previous Holocene study (Schmidt et al., subm.), we tested hypotheses about the processes controlling foraminiferal assemblage size variations in the late Quaternary with the following results:

1. The size response to temporal environmental changes during glacial-interglacial cycles mimics the spatial Holocene size variations. In the late Quaternary, as in the Holocene, large-scale planktic foraminiferal assemblage size variations are related to a temperature gradient, whereas fine-scale variations can be related to other factors such as productivity and environmental variability.
2. The amplitude of size change matches the extent of the climatic fluctuations, stable environment displaying the most limited assemblage size variation.
3. The impact of environmental changes on assemblage size variation can be mediated by to biological processes: species replacement and intraspecific size variation. Their relative importance depends on the environmental setting of the core. In the subtropics and tropics, represented by GeoB1413 and GeoB1105, the species have narrow ecological niches and species replacement is most likely to occur. In the subpolar environment, species have wider environmental preferences, but they still display intraspecific size decrease when moving out their ecological optimum. Therefore, intraspecific size changes without species replacement are more likely to occur in this environment.

The similarity of the results observed in both, the Holocene and late Quaternary records provide some evidence that the ecological preferences of the investigated species did not change much during the last 300 kyrs. Therefore, the assumption of an analogue situation for paleoceanographic reconstructions based on planktic foraminiferal temperature optima is supported by our results. Expanding our approach to a longer time record might permit the recognition of the beginning of a non-analogue situation, where the influence of evolutionary change would become the dominant factor.

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CHAPTER 5*

THE ROLE OF ENVIRONMENTAL CHANGES ON SIZE VARIABILITY OF PLANKTIC FORAMINIFERS DURING THE CENOZOIC

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Abstract

Repetitive evolution has been documented in foraminiferal morphology (Cifelli, 1969). Here we analyse the macroevolutionary processes involved in the size changes within the Cenozoic foraminiferal assemblage and evaluate relationships to paleo-environmental changes. 454 samples from subpolar to tropical environments were analysed. The maximum diameter of all specimens within the assemblage was measured to address the question of macroevolutionary change and its relationship to macroecology.

The size record in high latitudes is dominated by little size variability. In contrast, evolution of size in low latitudes can be divided in three major phases. The first, from the K/T boundary to 42 Ma is characterised by dwarfs. During a transition time from 42 to 14 Ma sizes there was a moderate increase in size with respect to the Paleogene. The last 14 Myrs were dominated by giants, with unprecedented large values in the last 10 Myrs.

The timing of these size increases can be related to global cooling, in particular to the latitudinal and vertical temperature gradients. A close relationship with the temperature differences between surface and bottom water is evident in the Neogene. In the Paleocene and during the Oligocene, productivity changes explain the size variability better. In these times of major reorganisation of global circulation of the ocean, diversity was reduced, and surface waters might have been biologically undersaturated with respect to surface dwelling species. The persisting species are thus reacting in size to changes in primary productivity.

5.1 INTRODUCTION

A major goal of modern paleobiology is the search for the physical boundary conditions of rates, magnitudes, and the spatial scales of biotic changes (Shackleton, 1984). It is still unclear if biotic or physical factors were more important in the initiation of speciation and extinction in the history of life. In the same context, the underlying causes for the radiations of form, which is defined by size and shape, remain major challenging questions in paleobiology (Caroll, 2001).

Marine sequences offer excellent material to study evolutionary processes. DSDP and ODP cores provide a number of continuous records with well-dated marine carbonate sequences, comprising large numbers of microfossils deposited in different water masses. One of the most abundant microfossil groups are the planktic foraminifers.

Planktic foraminiferal species have well-documented stratigraphic ranges and paleogeographic distribution (Bolli et al., 1985; Berggren et al., 1995) and phylogenetic relationships have been inferred for the most abundant and many minor forms (Kennett and Srinivasan, 1983; Bolli et al., 1985). Evolutionary changes can be analysed at two different scales: macroevolutionary changes are geared towards identifying general principles and/or broad patterns above the species level (Caroll, 2001). Microevolution, on the other hand, considers evolutionary change at or below the level of species and individual populations (Lazarus et al., 1995). Several different approaches have been used to study the evolution of foraminifers on both levels. These include species richness of the assemblage (Tappan and Loeblich, 1988), morphology of the whole group (Cifelli, 1969; Arnold et al., 1995), morphometry of lineages and species (Malmgren and Kennett, 1981; Arnold, 1983; Norris, 1996; Spencer-Cervato and Thierstein, 1997), the dynamics of origin and extinction of species (Thunell, 1981; Wei and Kennett, 1983) and biogeographic changes (Parker et al., 1999).

Three successive intervals of morphological diversification have been documented (Cifelli, 1969; Norris, 1991). At the beginning of each interval, planktic foraminifer assemblages consist of species with globigerinid (round, trochospirally arranged chambers) forms of generally small size (Luterbacher and Premoli-Silva, 1964). Larger species and species with keels evolved convergently after the K/T and the Eocene/Oligocene mass extinctions (Norris 1991). This iterative pattern is related to major changes in the structure of surface waters (Lipps, 1970; Cifelli, 1969). The horizontal and vertical thermal gradients of the seas are assumed to be responsible for the evolutionary pattern. Warm high-latitude climates eliminated thermally related mechanism of species maintenance, whereas, when these climates cooled, the thermal mechanisms intensify and the number of species increases (Lipps, 1970).

This study will concentrates on trends in the size of entire planktic foraminiferal assemblages. While size analysis of species and lineages are locally and ecologically restricted, a study of changes in the size of entire assemblage can give insights into macroevolutionary processes and their dependence on known global changes.

In Recent and Late Quaternary sediments, the size distribution of the entire foraminiferal assemblages (termed $\text{size}_{\text{assemblage5}}$) is closely related to patterns and changes in the physico-chemical processes of the ocean's surface waters (Schmidt et al., subm, Schmidt et al., in prep). Temperature-related effects have been identified as driving the main trend in assemblage size, causing an increase in size from the polar to the tropical biogeographic zones. However, regions of high environmental variability are characterised by smaller sizes than expected from the general size trend. The $\text{size}_{\text{assemblage5}}$ change can be interpreted as a result of two processes: size changes within single species and species replacement, both as reactions to environmental changes.

The Premises and aims of this study are as follows:

1. In the Holocene and Pleistocene, assemblage sizes are smaller in higher latitudes than in lower latitudes (Schmidt et al., subm.). Hence, cores from all major biogeographic regions will be compared to test and verify whether biogeographic size differentiation prevailed throughout the Cenozoic.
2. The morphological response is proportional to the environmental changes in the late Quaternary (Schmidt et al., in prep). The size change of entire foraminiferal assemblages thorugh time are related to the magnitude of temporal climatic fluctuations. During the Cenozoic, several major paleoceanographic changes have been documented and hence, size should vary in accord with these. We aim to test this relationship for the Cenozoic.
3. Following the Late Quaternary size paradigm discussed above, global climatic and paleoceano-graphic shifts should provoke globally synchronous size changes. We will compare records from all major basins to search for synchrony of variations in assemblage size.
4. If size changes are a direct consequence of paleoceanographic changes, we propose to trace Cenozoic environmental perturbations of different amplitudes and their related impact on foraminiferal macroevolution.
5. We test the hypothesised relationship between size and species richness. The size structure of an assemblage is related to the taxonomic composition of the assemblage and, thus, to the size distributions within each taxon (Schmidt et al., subm). Since species richness was changing over time with low diversity faunas in the Danian and Oligocene and high diversity in the Eocene and late Neogene, a correlation of size and species richness might be expected.

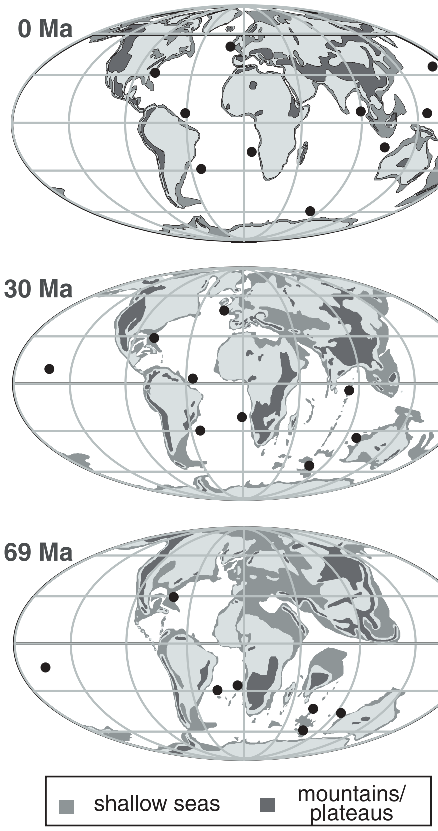
5.2 MATERIAL AND METHODS

We selected DSDP and ODP cores from low to high latitudes (Fig. 5.1) and from the three major oceans (Table 5.1). We gave preference to samples with high carbonate contents to insure good preservation and aimed for sites spanning the whole Cenozoic without major hiati. All together we analysed 454 samples. Age models are based on the references in Table 5.1 and all have been adjusted to Berggren et al. (1995).

Table 5.1: Overview about selected cores for the study. ATL = Atlantic, IND = Indic, PAZ = Pacific, SO = Southern Ocean, N = number of measured samples. LSR= Linear sedimentation rate.

Location	DSDP/ODP sites	Ocean	N	Zone	Age Range	LSR	Age model
Walvis Ridge	Leg 40, 362	ATL	13	temperate	1.8 – 23.7	32.0	Lazarus et al. 1995
	Leg 40, 363		27		24.4 – 72.0	7.21	Spencer-Cervato, 1999
Rio Grande Rise	Leg 72, 516	ATL	20	subtropical	0.8 – 21.5	8.22	Pujol, 1983
	Leg 72, 516F		34		21.9 – 64.7	18.5	Spencer-Cervato, 1999
Walvis Ridge	Leg 74, 522	ATL		subtropical	56.3 – 65.2	5.9	
Goban Spur	Leg 80, 548A	ATL	34	temperate	0.1 – 53.4	8.8	Knappertsbusch pers.com.
Kerguelen Plateau	Leg 120, 738B, C	SO	26	subpolar	0.0 –27.7	5.8	Spencer-Cervato, 1999
	Leg 120, 747A, C						Lazarus et al. 1995
	Leg 120, 748B, C						Lazarus et al. 1995
	Leg 120, 750						
Ninetyeast Ridge	Leg 121, 758	IND		tropical	0.3 – 69.5	4.9	Peirce et al., 1989
Exmouth Plateau	Leg 122, 762B	IND	23	subtropical	0.0 – 32.2	5.3	Spencer-Cervato, 1999
	Leg 122, 762C		15	subtropical	34.2 – 70.2	11.6	
Ontong Java Plateau	Leg 130, 806B	PAC	39	tropical	0.2 – 23.1	31.2	Chaisson and Leckie, 1993 SC 1999
Allison Guyot	Leg 143, 865B	PAC	28	subtropical	4.7 – 55.2	2.0	Bralower and Mutterlose, 1995 Sliter, 1995
	Leg 143, 865C		3	subtropical	19.7 – 34.5	1.4	
Ceara Rise	Leg 154, 925A, B	ATL	23	tropical	13.5 – 43.2	23.6	Compiled from Pearson and Chaisson, 1997 Chaisson and Pearson, 1997 Shackleton et al., 1999
	Leg 154, 925B		16	tropical	0.0 – 14.0	22.6	
	Leg 154, 929A		10	tropical	33.3 – 56.1	14	
	Leg 154, 929E			tropical			
Blake Nose	Leg171B, 1049	ATL		Subtropical			Norris et al. 1998
	Leg171B, 1050			Subtropical			Rudnicki et al., 2001
	Leg171B, 1051			Subtropical			

Foraminiferal assemblage size has been shown to depend on the position of the samples along the temperature gradient in the Holocene and late Quaternary (Schmidt et al., subm.; Schmidt et al., in prep.). Based on this result, the analysed cores have been grouped into subpolar, temperate, subtropical and tropical environments according to their biogeographic provenance. Biogeographic zonations are based on plate tectonic reconstructions, on faunal compositions reported in the relevant DSDP/ODP initial results and on the assumption of latitudinal faunal changes persisting over time. This oversimplification ignores the fact that biogeographic gradients during the early Cenozoic might have been small (Jenkins, 1985). Additionally, the two sites from the Ninetyeast Ridge (ODP Site 758) and Exmouth Plateau (ODP Site 762) strongly changed their paleo-latitude over time. ODP Site 758 moved from a subtropical position in the Paleogene (Shipboard Scientific Party, 1989) to tropical position since the early Oligocene and ODP Site 762 from temperature to subtropical (Shipboard Scientific Party, 1990) in the same time interval. These sites are grouped within tropical (Site 758) and subtropical (Site 762) biogeographic zones.



Maps modified after Zachos at al (2001)

Figure 5.1: Paleogeographic reconstructions modified after Zachos et al. (2001). Black dots represent the location of the cores sampled for each time interval. Locations are based upon “Advanced plate tectonic reconstructions, http://www.ODSN.de”.

A representative split of the size fraction >150µm was analysed for each of the 454 samples (mean of 2293 individuals, minimum 650, maximum 6273 individuals), in total 1.041.022 measurements. It was possible to determine the assembly of such a large morphometric data set by applying a system for automated microscopy and test outline extraction (Bollmann et al., subm). Size parameters of randomly oriented foraminifers were measured. The maximum diameter of the object was chosen as the most suitable size estimator because it is least affected by random orientation. The accuracy of diameter determination at the applied magnification of 160x is 3.31 µm per pixel. The sizes of individuals within a foraminiferal assemblage have an exponential distribution (Schmidt et al., subm.). The minimum size in our data set is given by the sieve size (>150µm). It represents an artificial cut-off of the natural size distribution and, therefore, does not have any biological significance. Since the distributions are highly skewed towards large size, the best descriptors of the distributions are the 95-percentile of the assemblage ($size_{assemblage5}$) and the maximum (see Schmidt et al., subm for discussion). Here, we use changes in the 95-percentile of the sizes in the entire foraminiferal assemblage termed $size_{assemblage5}$ to describe the variance of size, a procedure that has been successfully applied to amphipods (Chapelle and Peck, 1999).

Based on the Holocene calibration, we tested the influences of both physico-chemical and biological processes. The physico-chemical processes are characterised by paleo-temperature and paleo-productivity proxies. Proxies for biotic interactions are species richness and intraspecific size change in species or lineages. The evolution of food sources, such as copepods, and of predators cannot be quantified due to the lack of data. We use $\delta^{18}0$ and Mg/Ca-ratios as proxies for temperature (Lear et al., 2000; Zachos et al., 2001) and $\delta^{13}C$ for changes in the paleo-productivity of the ocean (Zachos et al., 2001). Oxygen isotope fractionation between seawater and the carbonate ions (CO_3) that are incorporated into the shell lattice is influenced by temperature and the isotopic composition of sea water. This dual control on shell $\delta^{18}O$ complicates the interpretation of trends over those intervals when large ice-sheets are present (Zachos et al., 2001). As a measure of water stratification, we complied $\delta^{18}0$ records of surface-dwelling planktic foraminifers from the tropic, subtropic and temperate realm and calculated their offsets from the global benthic $\delta^{18}0$ records (see Table 5.2 for references). A large difference in benthic and planktic $\delta^{18}0$ values ($\Delta\delta^{18}0_{benthic-planktic}$) indicates temperature differences between the source of deep-water and the surface water at the site. During the Cenozoic, deep-water was formed at high latitudes. Consequently, $\Delta\delta^{18}0_{benthic-planktic}$ provides information about the temperature difference between high-and low latitudes and between deep- and surface waters. We were able to compile stratification data for the entire Cenozoic in the subtropics, the past 50 Myrs in the temperate region and the last 24 Myrs in the tropics. During times of major ice built-up, e.g. at the Eocene-Oligocene boundary and the Mid-Miocene, changes in $\delta^{18}0$ in benthic foraminifers represent, to a large degree, changes in ice volume and not temperature (Lear et al., 2000). The $\Delta\delta^{18}0$ values have been compared to the regional size record of the subpolar, temperate, subtropical and tropical environments (5-point moving average of all records of this regions).

The stable carbon isotope ratio ($^{13}C/^{12}C$) of benthic foraminifers largely reflects the isotope ratio of the total dissolved inorganic carbon (DIC) of ambient seawater, which varies in response to fluctuations in the major fluxes of global carbon cycle (Shackleton, 1987). Algal organic matter is isotopically light (<-20‰) due to the preferential uptake of ^{12}C during photosynthesis. If organic carbon burial increases, it should drive the $\delta^{13}C$ value of the remaining DIC higher, assuming other fluxes remain fixed. Similarly, sustained changes in the flux of carbon into the ocean from continental weathering and volcanic outgassing can alter mean ocean $\delta^{13}C_{DIC}$ values (Zachos et al., 2001). Models estimate a gradual increase in weathering of continental organic material from the early Paleocene to the Miocene, followed by a dramatic increase in the last 15 Myrs (Wallmann, 2001). Burial rate of organic matter during the Cenozoic has been cyclic, with periods of higher values occurring around 58 Ma, 25 Ma and during the last 14 Myrs, which show a dramatic increase (Wallmann, 2001).

Table 5.2: Sites selected for the compilation of isotope data for calculation of $\Delta\delta^{18}0$.

Leg or Site	Location	Interval	Species	Reference
Benthic	Global	0-70	Multiple species	Zachos et al., 2001
173	North Pacific	9-14	*G. bulloides*	Barrera et al., 1985
237	Equatorial Indic		*D. altispira*	Savin et al. 1985
238	Equatorial Indic		*G. sacculifer, D. altispira*	Savin et al. 1985
253	90 East Ridge		planktic	Oberhänsli, 1986
310	North Pacific	5-14	*O. universa*	Savin et al. 1985
366A	Equatorial Atlantic	10-22	planktic	Savin et al. 1985
Leg74	Walvis Ridge	0-65	Multiple species	Shackleton et al., 1984
806B	Ontong Java	0-1	*G. sacculifer*	Berger et al., 1996
		3-5	*G. sacculifer*	Jansen et al., 1993
		Miocene.	*D. altipira, Gq. venenezuelana, G. sacculifer*	Gasperi and Kennett, 1993
586 586A		Plio/Pleist	*G. sacculifer*	Whitman and Berger, 1993
289	Ontong Java	5-19		Savin et al. 1985
Leg154	Ceara Rise	Mio-Plei	Multiple species	Chaisson and Ravelo, 1997
		Mio	*G. sacculifer, G. ruber*	Pearson et al., 1997
		Mio	*Gs. prim*	Paul et al., 2000)
			Multiple species	Pearson et al., 2001
354	Ceara Rise	15-25	*G. venezuelana*	Biolzi, 1985)
277, 593, 592	Tasman Basin	30-42	*G. angiporoides*	Murphy and Kennett, 1986
588. 590 591	Tasman Basin	2-22	*quadrilobatus-immaturis-sacculifer* complex	Kennett and Borch, 1986
522	South Atlantic	Eo/Oli	Multiple species	Poore and Matthews, 1984

The data for species richness, which changes as a result of differences between speciation rates and extinction rates, is taken from compilations by Wei and Kennett (1986), Bolli et al. (1985), Thunell (1981), and Norris (1991).

5.3 RESULTS

The two main features of the macroevolutionary Cenozoic size record are the sudden decrease at the K/T boundary and the dramatic increase during the late Neogene in low latitudes (Fig. 5.2). Planktic foraminiferal sizes are larger in the Pliocene/Pleistocene than they have ever been in the last 70 Myrs. The observed $\text{size}_{\text{assemblage5}}$ changes are presented and discussed at several scales: locally at one site, regionally within a biogeographic zone (e.g. the tropics) and globally.

At the K/T boundary, a reduction of $\text{size}_{\text{assemblage5}}$ of about 150µm is found at the Walvis Ridge, Site 527 and Kerguelen Plateau, Site 750. The large Maastrichtian sizes are never reached again by foraminifers growing at high latitudes. The reappearance of comparably large sizes in mid- and low latitudes is delayed until the late Neogene. The size records in high latitudes (Kerguelen Plateau, Rockall Plateau and Walvis Ridge) display an amazing stability and they remain around the Cenozoic overall size-average throughout the entire Cenozoic. An exception to this is observed from 22 to 15 Ma at the Kerguelen sites, where sizes increase significantly. This fluctuation is consistent with variations in coccolithophorid composition at Kerguelen Plateau, which have been attributed to movement of the subtropical front and immigration of subtropical organisms (Beaufort and Aubry, 1990). We assume that the same process also brought foraminifers from warmer areas to this site which are larger than those of cold ones.

In mid- to low latitude areas (Rio Grande Rise, Allison Guyot, Ceara Rise) size increased during the Middle Eocene to the Late Oligocene. A strong size increase started around 20 Ma at tropic sites (Ninety East Ridge, Ceara Rise, Ontong Java) and around the Pliocene/Pleistocene boundary at the subtropical sites (Rio Grande Rise, Exmouth Plateau) (Fig. 5.2).

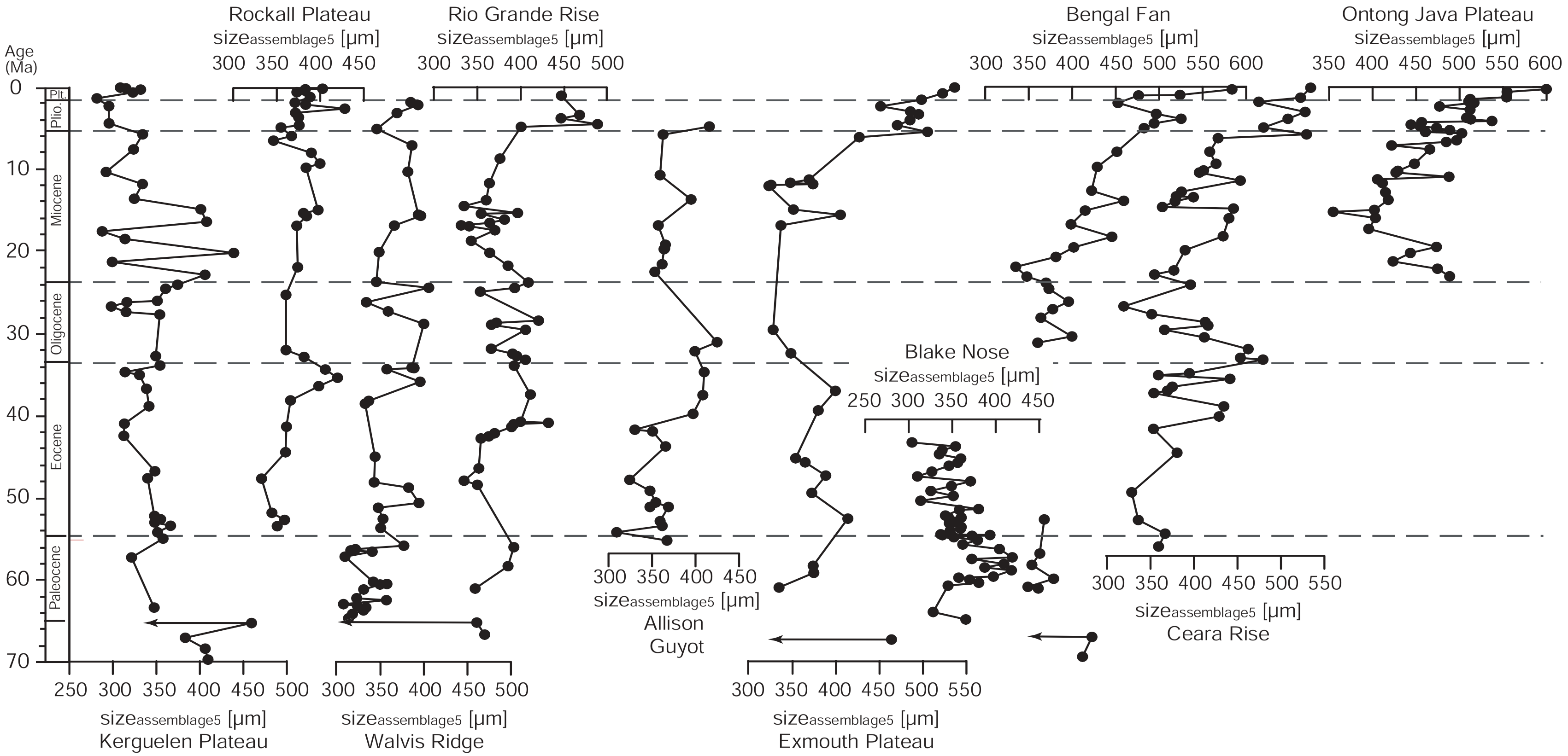


Figure 5.2: $\text{Size}_{\text{assemblage5}}$ of all measured sampels. Cores arranged according to their Neogene latitude from high (right) to low latitudes (left). Dashed lines indicate stage boundaries (Berggren et al, 1995).

5.3.1. Global size pattern: high versus low latitudes

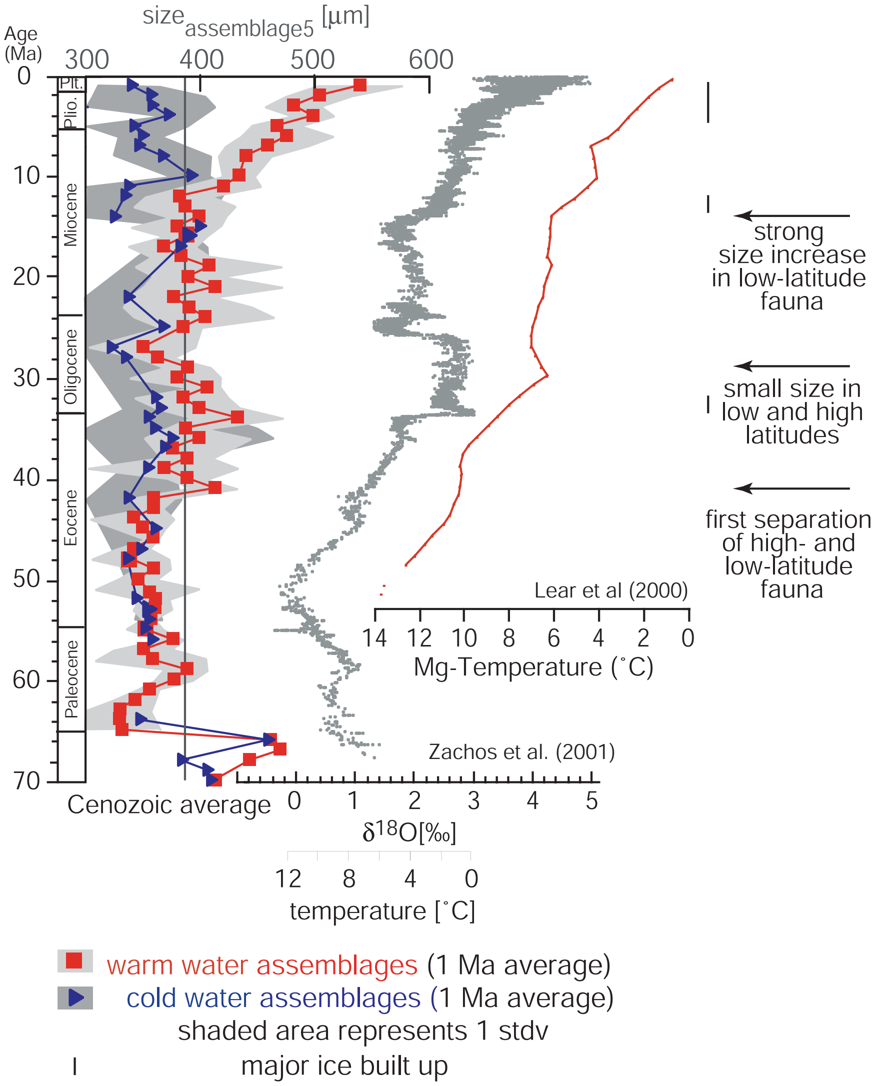


Figure 5.3: Size$_{assemblage5}$ of high latitudes (subpolar to temperate cores) and low latitudes (subtropical and tropical) compared to $\delta^{18}0_{benthic}$ (Zachos et al., 2001) and Mg/Ca temperatures (Lear et al., 2000). The shaded area represents one standard deviation from the mean of size$_{assemblage5}$ for high latitudes (dark grey) and low latitudes (light grey). The grey line represents the Cenozoic average of the entire data set. The black vertical lines indicate major ice built-up.

Large-scale distribution patterns are revealed by a comparison of the one million year averages of all cold (subpolar and temperate) versus all warm (subtropical and tropical) size records (Fig. 5.3). Three intervals appear discernible: a period of “dwarfs” (diameters below 390 µm in both cold and warm environments, lasting from 65 to 42 Ma, a transition time with values around the Cenozoic mean of 389 µm)(diamter in high latitudes: 245-405µm; low latitudes: 35 -430µm) from 42 to 14 Ma and a period of giants at low latitudes with values up to 540 µm in the last 14 Myrs (Fig. 5.3). The Cenozoic starts with a size reduction related to the mass extinction at the K/T boundary in both, high and low-latitudes. In the early Cenozoic up to approximately 42

Ma, size$_{assemblage5}$ high and low latitude samples cluster around 312 to 360 µm with a narrow range (Fig. 5.3). The exception is a size increase up to 390 µm from 60 to 55 Ma driven by the record of Blake Nose, which will be discussed later in detail. Test sizes comparable to those of the Late Maastrichtian were not found in any of the studied Paleogene samples.

Around 42 Ma, sizes start increasing globally with a larger increase in low than in high latitudes. The increase in size leads to values above the average size, 389µm, of all Cenozoic samples (Fig. 5.3). The values at all latitudes fall back to early Paleocene ranges between 29 and 26 Ma. The reduction is stronger in low latitudes, which results in small latitudinal size gradients in the Late Oligocene and early Miocene. Around 14 Ma, the dramatic increase in size in the warmer waters leads to a definite separation of the two trends and unprecedented large sizes in the low latitudes since the Pleistocene. The difference between low and high latitude sizes increases by a factor of 5 from the Late Oligocene to the Pleistocene.

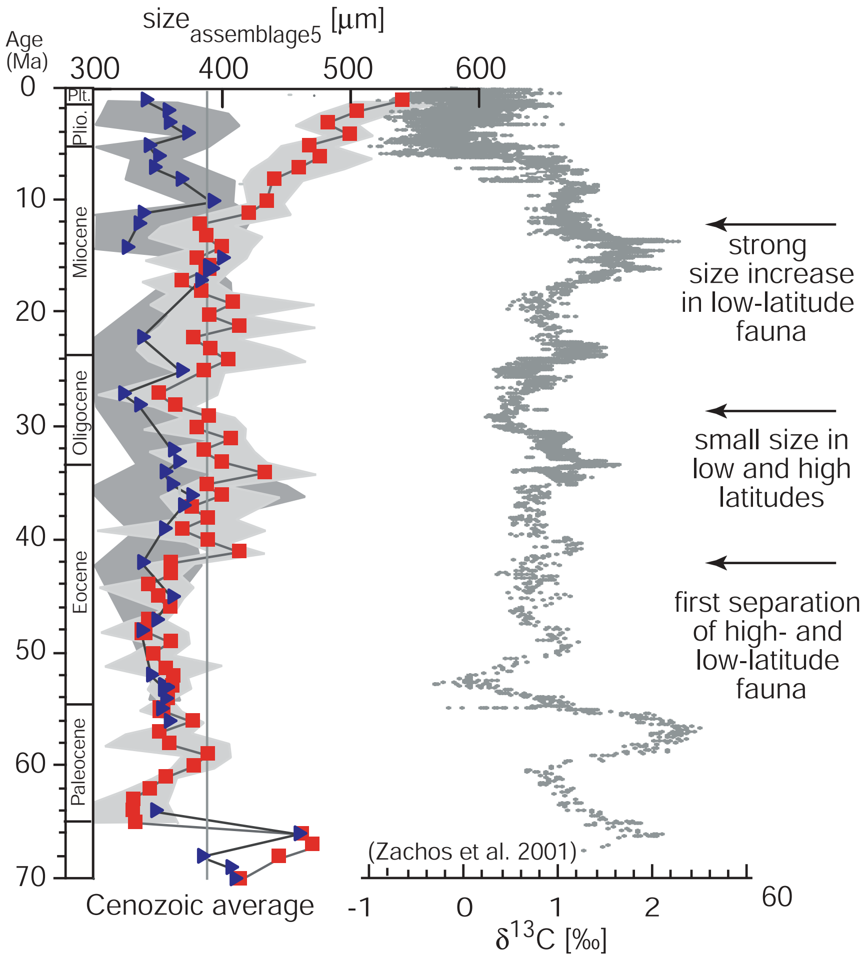


Figure 5.4: Size$_{assemblage5}$ of high latitudes (subpolar/temperate cores) and low latitudes (subtropical/tropical) compared to $\delta^{13}C$ of benthic foraminifers (Zachos et al., 2001). The shaded area represents one standard deviation from the mean of size$_{assemblage5}$ for high latitudes (dark grey) and low latitudes (light grey). The grey line represents the Cenozoic average of the entire data set. Legend see Fig. 5.3.

5.3.2 Comparison with physico-chemical and biological proxies

To understand the potential causes for the observed size trends, we compared them with variations in $\delta^{18}0$, $\delta^{13}C$ and species richness. At first glance, size$_{\text{assemblage5}}$ and $\delta^{18}0_{\text{benthic}}$ seem to vary in accord with each other during several time intervals (Fig. 5.3). Less positive $\delta^{18}0_{\text{benthic}}$ values and high Mg/Ca-temperatures are associated with smaller sizes. At low latitudes, more positive $\delta^{18}0_{\text{benthic}}$ values and low Mg/Ca-temperatures are associated with larger sizes. The dramatic gradual size increase in low latitudes in the Late Neogene parallels an equally gradual increase in $\delta^{18}0_{\text{benthic}}$ values and decreases in Mg/Ca-temperatures, which can be interpreted as decreasing temperatures associated with larger test size in the low latitudes. This temperature-size relationship does not hold during the entire Cenozoic. Particularly in the Paleogene and Oligocene, other environmental parameters are apparently related to the observed size changes.

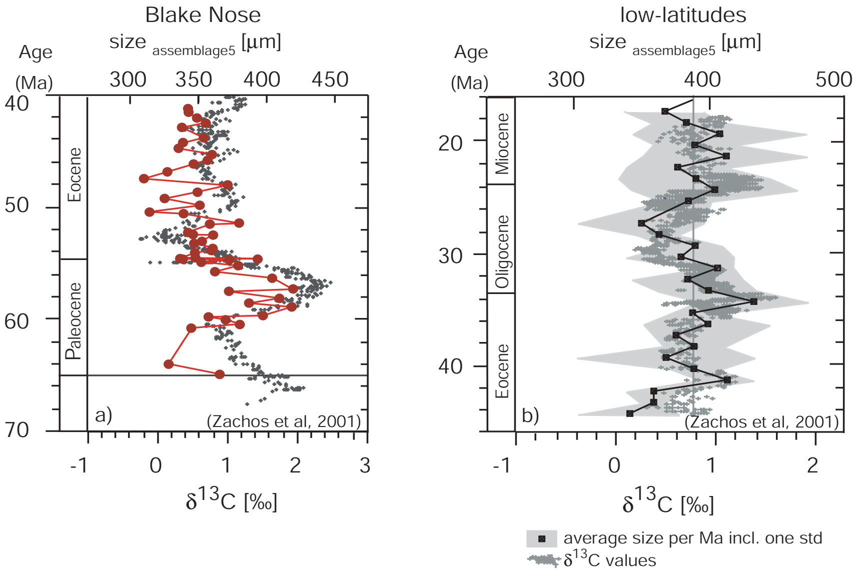


Figure 5.5: a) Paleogene comparison of size$_{\text{assemblage5}}$ from a single site (Blake Nose, Leg 171B, circles) and $\delta^{13}C$ of benthic foraminifers (global compilation, Zachos et al. (2001)); **b)** Late Eocene to early Miocene compilation of subtropical/tropical size$_{\text{assemblage5}}$ (squares) compared to $\delta^{13}C$ of benthic foraminifers (global compilation, Zachos et al., 2001). The shaded area (light grey) represents one standard deviation from the mean of size$_{\text{assemblage5}}$ for the low-latitude records and the dark grey dots $\delta^{13}C$.

The early Paleogene size record is well correlated to the $\delta^{13}C$ change (Fig. 5.4). To show this feature more clearly, we compare the size record at Blake Nose, where we have the highest Paleogene resolution, with the global $\delta^{13}C$ record. Larger sizes (Fig 5.5a) are accompanied by higher $\delta^{13}C$ values, indicating times of high carbon burial. The major Paleocene fluctuations are well correlated in both records from the K/T boundary to 50 Ma (Fig. 5a). From 50 to 40 Ma, $\delta^{13}C$ values are rather constant, and consequently cannot be responsible for the size increase around 42 Ma (Fig. 5.4). In the Late Eocene to Early Miocene, there seems to be also an overall correlation between $\delta^{13}C_{benthic}$ and size (Fig. 5.5b).

Why are sizes correlated with $\delta^{13}C$ rather than with $\delta^{18}0$ in the Paleocene and Oligocene? What is the major difference between assemblage from these two intervals compared to the rest of the Cenozoic? Next to physico-chemical properties of the ocean, biological characteristics also change, e.g., the species richness. An increase in species richness would lead to a higher probability for the inclusion of species reaching large size within the assemblage.

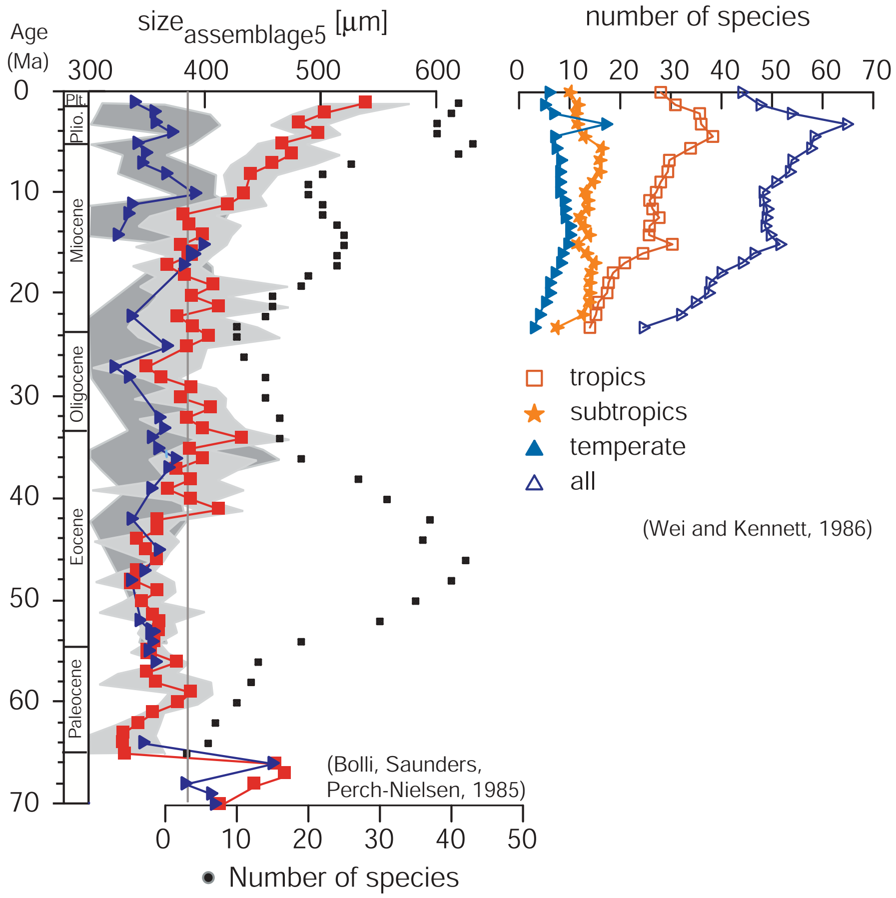


Figure 5.6: Size$_{assemblage5}$ of high latitudes (subpolar to temperate cores) and low latitudes (subtropical and tropical) compared to species richness (black squares; J.-P. Beckmann unpublished based on Bolli et al., 1985). The Wei and Kennett (1986) compilation is separated into biogeographic regions. Legend see figure 5.3.

In general, there is no correlation between size and species richness (Fig. 5.6) except for the Neogene, where both records show a general increase, but without clear correlations. The dramatic increase in species richness in the Eocene is not paralleled by size. Despite this lack of correlation, total species richness is generally higher during times with a size-temperature relationship (Eocene, Neogene) and generally lower during the intervals with a size-$\delta^{13}C$ relationship. We have no explanation for these changes.

5.3.3 Biogeography, size and the structure of the water column

It is not entirely unexpected to find a correlation of $\text{size}_{\text{assemblage5}}$ in low latitudes and the global benthic $\delta^{18}0$ curve (Lipps, 1970). A change in $\delta^{18}0_{\text{benthic}}$ indicates cooling or warming in the source regions of the bottom waters. Hence, the relationship of low-latitude $\text{size}_{\text{assemblage5}}$ and $\delta^{18}0_{\text{benthic}}$ could be related to the influence of vertical and latitudinal temperature gradients on $\text{size}_{\text{assemblage5}}$.

The size in subpolar assemblages has been gradually decreasing in the past 70 Myrs, albeit within a narrow size range. The planktic foraminiferal size range in temperate environments is also very restricted, consistent with only minor variations in the $\Delta\delta^{18}0_{\text{benthic-planktic}}$ (Figure 5.7). Despite the low variability, the intervals of increasing size and times of stability are in agreement with $\Delta\delta^{18}0_{\text{benthic-planktic}}$ changes (dashed line in Fig. 5.7).

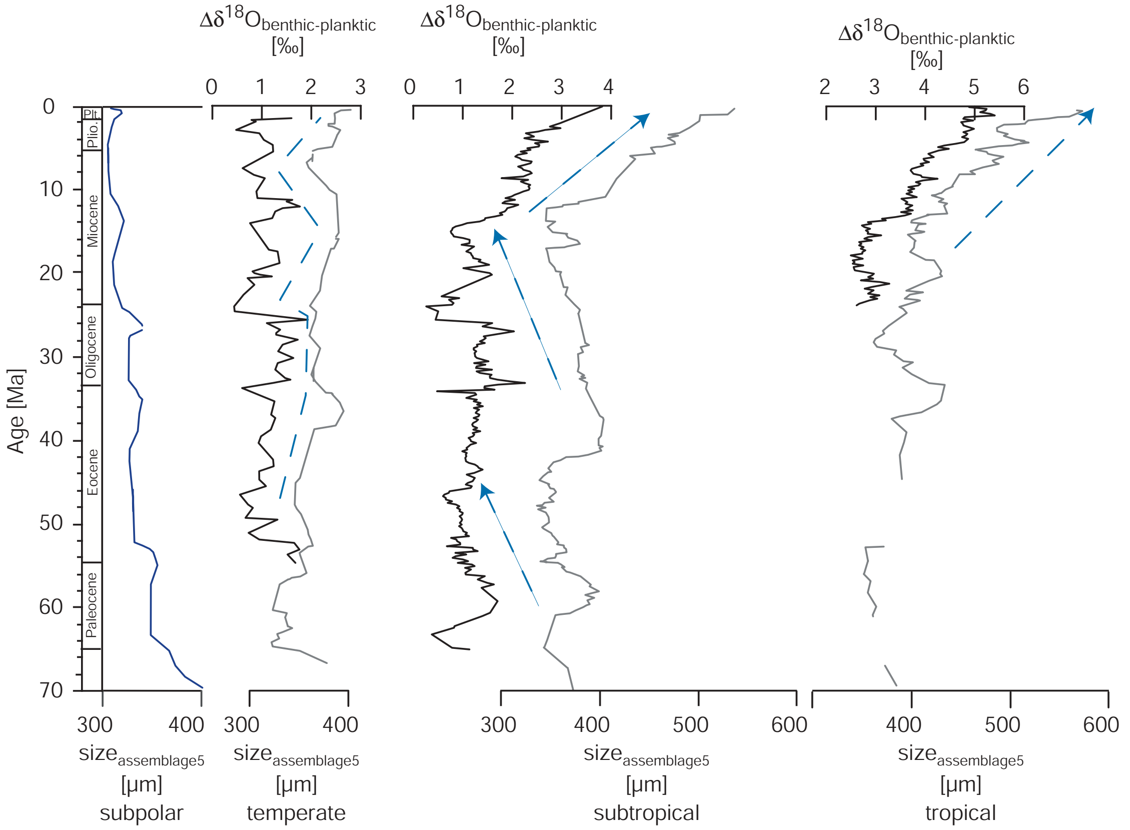


Figure 5.7: 5-point moving average of $\text{size}_{\text{assemblage5}}$ (grey lines) pooled per biogeographic zone (subpolar, temperature, subtropical, tropical). The black line represents $\Delta\delta^{18}0_{\text{benthic- planktic}}$ for the biogeographic zones (references see table 5.2) and the dashed arrows mark similar trends in size and $\Delta\delta^{18}0_{\text{benthic- planktic}}$.

Larger changes in size and $\Delta\delta^{18}0$ are characteristic for the environments at low latitudes. In the subtropics, $\Delta\delta^{18}0$ and size trends are parallel during the Late Paleocene to Mid-Eocene, the Oligocene and from the Mid-Miocene till recent. The same holds true for the late Neogene tropical records. However, despite the general agreement of the overall trends, many smaller features in both records are asynchronous or sometimes inversely correlated. Changing correlation may be caused by several effects and processes: the different resolution of both records, the biased selection of cores for both compilations, regional trends in size or temperature, and/or short term fluctuations in the isotopes (e.g. Berger et al., 1996) and/or the size records (Schmidt et al., in prep).

5.3.4 Local correlation of size and oxygen isotopes

To analyse the details of leads, lags and mismatches between size and isotope records, planktic $\delta^{18}0$ records are compared with $\text{size}_{\text{assemblage5}}$ at Ontong Java in the Neogene (Fig. 5.8).

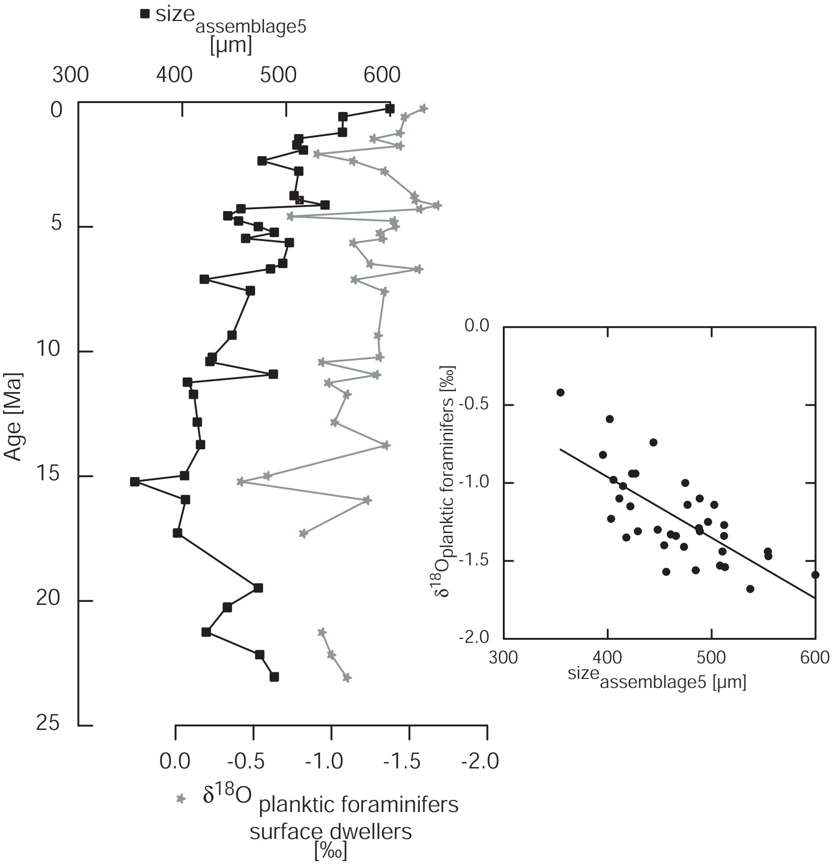


Figure 5.8: $\text{Size}_{\text{assemblage5}}$ of Ontong Java (black squares) compared to subsampled oxygen isotope data-set of Ontong Java (stars). Subsamples of isotope values are taken from the most similar time interval. For references see table 5.2., inlet: Linear correlation of $\text{size}_{\text{assemblage5}}$ and oxygen isotopes at Ontong Java. r = 0.718, $r^2 = 0.516$, $p = 0.000$.

$\delta^{18}0$-values display a large variability related to climatic change. Consequently, the resolution of the oxygen isotope record was reduced to match the one of the size record. Size$_{\text{assemblage5}}$ values are compared to the isotope values of most similar age, with a maximum difference of 200 kyrs. The two records are similar to each other over the entire range of 23 Myrs (Fig. 5.8). The correlation of size and $\delta^{18}0$ shows a clear trend (Fig. 5.8, $r = 0.781$, $p = 0.000$). The residual variability might be related to additional influences on $\delta^{18}0$ values of multiple planktic foraminifers such as changes in the isotopic composition of sea water, vital effects, preservation. Specifically, the increasing ice volume around 14 and 4.6 Ma must have changed the $\delta^{18}0$ of the seawater. In the future, size$_{\text{assemblage5}}$ and isotopes should be measured in the same samples.

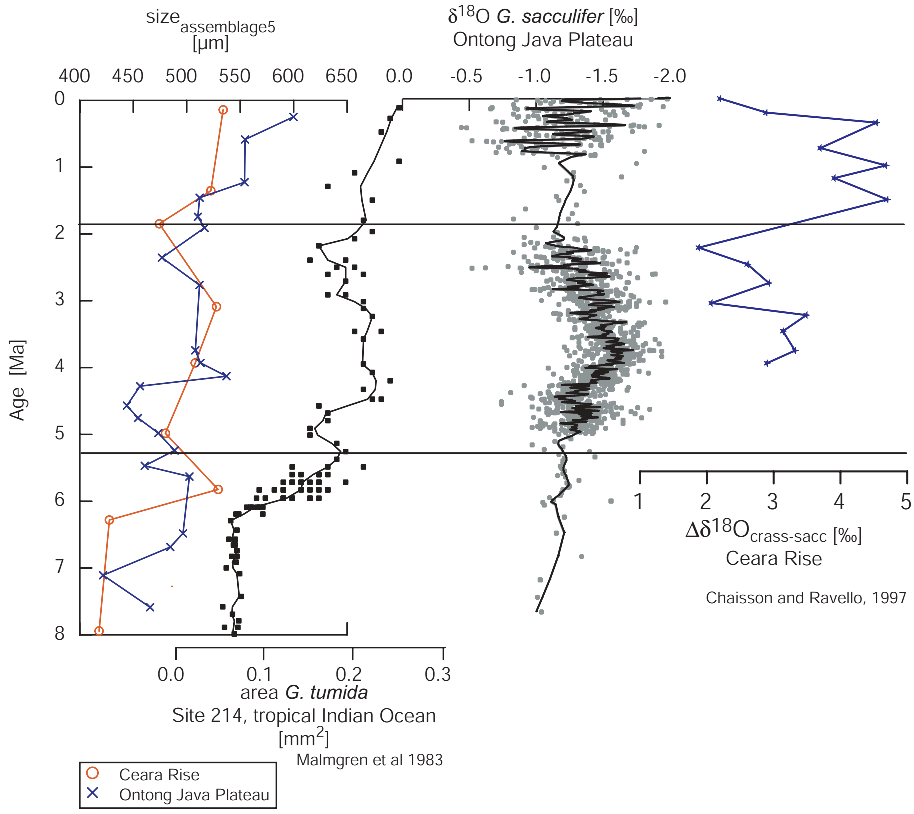


Figure 5.9: Size$_{\text{assemblage5}}$ of Ontong Java (crosses) and Ceara Rise (circles), compared to low-latitude single size records (*G. tumida*, Site 214, equatorial Indian Ocean, Malmgren et al., 1983), oxygen isotopes of Ontong Java (references see table 5.2) and stratification as indicated by $\Delta\delta^{18}0$ of *G. crassaformis* and *G. sacculifer* at Ceara Rise (Chaisson and Ravello, 1997).

Changes in assemblage size can be a result of intraspecific and interspecific size changes. To survey a possible relationship, we compare two tropical assemblage-size records from the Atlantic (Ceara Rise) and the Pacific (Ontong Java Plateau) to a single-lineage size record, *G. tumida* lineage, from the tropical Indian Ocean (Site 214) (Fig. 5.9). These size records are compared to $\delta^{18}0$ of surface dwelling foraminifers, mostly *G. sacculifer*. Increasing assemblage size is associated with larger size within the *G. tumida* lineage and negative isotope values. Small differences in oxygen isotope between deep and shallow dwelling foraminifers seem to be related to small sizes. Hence, similar processes seem to drive assemblage size records and sizes changes in this lineage.

5.4 DISCUSSION

We identified temperature, fertility/carbon burial and species richness as the most likely factors influencing the $\text{size}_{\text{assemblage5}}$ record throughout the Cenozoic. We have shown that the relationship between these factors and size seems to vary over time. Hence, the paleo-proxy records and the faunal evidence will be discussed in a stratigraphic order. Other influences such as light attenuation, salinity or dissolved oxygen, which define the structure of niches, may play a role in species distribution and ecological subdivisions (see Norris, 2000 for further discussion). These parameters are not quantifiable over the Cenozoic and their potential influence on geographic size patterns is discussed in Schmidt et al. (subm.)

5.4.1 Reduction and recovery at the K/T mass-extinction event

The K/T event radically changed the open marine ecosystems including planktic foraminifers. 90% of planktic foraminiferal species went extinct at or shortly after the event (D' Hondt et al., 1996) which resulted in the disappearance of the late Cretaceous shelf-offshore provincialism of low- and mid-latitude faunas. The extinction included all large taxa such a *Globotruncana, Contusotruncana, Racemiguembelina, Planoglobulina.* The Danian fauna was composed of small and simple forms (Luterbacher and Premoli-Silva, 1964), as confirmed by our own size measurements from Sites 750, 527, 762 and 758. The faunal and floral reorganisation comprised a massive reduction in the number and size of planktic foraminifers and in coccolith abundance (Pospichal, 1996). Consequently, it led to a several-fold decrease in biogenic carbonate accumulation rates and a collapse of vertical carbon isotope gradients (Shackleton et al., 1984). This geochemical anomaly is thought to reflect a near-complete cessation of global marine productivity caused by the rapid demise of plankton (D' Hondt et al., 1998), and the absence of large grazers and/or the decrease in the mean size of primary producers (D' Hondt et al., 1998). The recovery of marine biota progressed slowly. Recovery of net productivity began 0.5 My after the boundary (Zachos et al., 1989). The recovery of the flux of organic material took more than 3 Myrs (D' Hondt et al., 1998). The low productivity is consistent with low rates of evolution within the foraminifers (Corfield and Shackleton, 1988) and small $\mathrm{size}_{\mathrm{assemblage5}}$ within the foraminiferal assemblages (Fig. 5.10). Corfield and Shackleton hypothesised that primary productivity controlled the evolution of planktic foraminifers after the K/T boundary (Corfield and Shackleton, 1988). We also assume that changes in productivity influenced the $\mathrm{size}_{\mathrm{assemblage5}}$ record at the beginning of the Paleocene.

5.4.2 Paleocene

The increase in taxonomic turnover, which is indicated by a rise in species richness, is related to a diversification of the morozovellids, which started at 62 Ma and peaked at 60.8 (Fig. 5.10). This genus was an important component of low and mid latitudes and represented the first step in the re-establishment of complex morphologies (Corfield and Granlund, 1988). Morozovellids are usually large (Kelly et al., 2001), symbiont bearing (Shackleton et al., 1985, D’Hondt 1994), morphologically specialised forms that predominated in the warm oligotrophic gyre systems (Boersma et al., 1998). The evolution of the morozovellids might have been controlled by the gradually increasing productivity (Corfield and Shackleton, 1988). This model is consistent with the fact that size, species richness and $\delta^{13}C$ are well correlated with each other (Fig. 5.10). The latitudinal temperature gradient was much lower during the Paleogene than at present (Savin et al., 1975; Shackleton and Kennett, 1975), explaining why temperature did not seem to have had an influence on the early Paleocene foraminiferal sizes.

The decrease in Morozovella species richness in the latest Paleocene to early Eocene was coherent with a reduction in size within the morozovellids. Although morozovellids were replaced by acarininids in this interval (Corfield and Shackleton, 1988) and some acarininids also developed to large adult sizes (Kelly et al., 2001), the size of the entire planktic foraminiferal assemblage remained parallel to the decline in species richness and size reduction of morozovellids. We see no conflict with Kelly et al.' s (2001) proposal that the cooling of tropical surface-waters was the cause for the progenesis in the morozovellids. Depth stratification of planktic foraminifers comparable to the Cretaceous was re-established in the Late Paleocene (Corfield and Granlund, 1988). During that time, the similarity between size and $\delta^{13}C$ trends is lost.

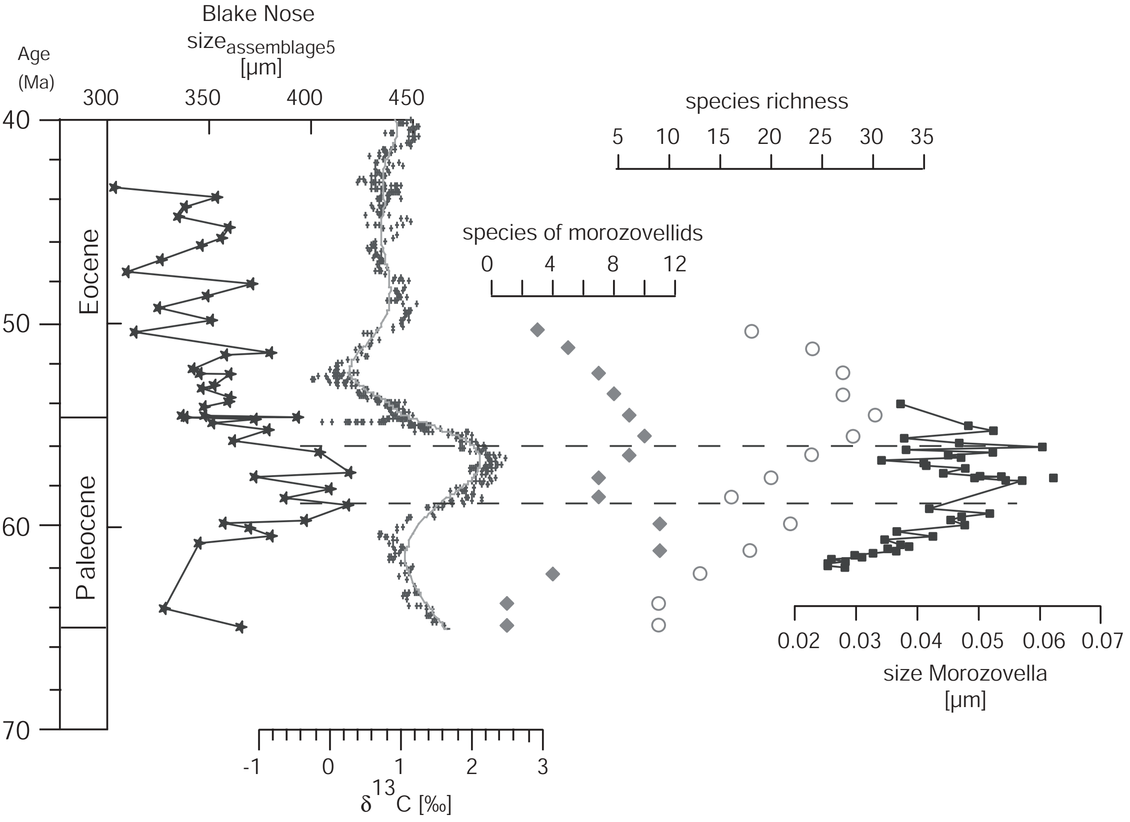


Figure 5.10: Paleogene record of size$_{assemblage5}$ at Blake Nose (stars) compared to δ^{13}C of benthic foraminifers, global compilation (Zachos et al., 2001), species richness of morozovellids (diamonds) and foraminifers in general (open circles) (Corfield and Shackleton, 1988), both complied from sites 577 (Shatsky Rise) and 527 (mid-latitude Atlantic), and size of morozovellids (squares) from the site 577, Shatsky Rise (Corfield and Granlund, 1988).

5.4.3 Eocene: Similarity of the regional size records

Changes in the composition of the foraminiferal assemblages indicate a transition from a moderately well mixed, warm ocean with marked thermal gradients, and relatively high fertility in the Paleogene to a poorly mixed ocean with low vertical and geographic thermal gradients and reduced fertility in the Early Eocene (Boersma et al., 1998). During the Early Eocene, the warmest Cenozoic interval, deep-water temperatures were around 13°C and thermal gradients were low (Barrera et al., 1987). Tropical temperatures may have been comparable to or warmer than today (Pearson et al., 2001). There is no oxygen isotopic evidence of a thermocline in the mid-latitudes during the Mid-Eocene (Muza et al., 1983). Stratification was poorly developed and species from different water masses were well mixed. Tropical species reached up to Antarctica (Boersma et al., 1998) and up to 55° North (Boersma et al., 1987). The presence of tropical species at high latitudes, either reproducing there or transported into these environments, influenced the size$_{\text{assemblage5}}$ in the investigated cores.

During the Early and Mid-Eocene, sizes were relatively small at all latitudes (Fig. 5.3). This is a good example that not high temperature (as suggested by Cifelli, 1969), but strong vertical gradients with a large number of niches, led to the large size$_{\text{assemblage5}}$, since the temperatures have been the highest in the Cenozoic (Zachos et al., 2001). The uniform climate led to an equitable, cosmopolitan fauna (Boersma and Premoli Silva, 1991). The similarity of the fauna is coherent with the resemblance of the size ranges from all latitudes.

The species diversity in the Eocene is comparably high as that in the Neogene. It has been suggested that size is related to an increase in variance and, consequently, to a larger number of species in an assemblage, which also increases the probability of large species to be included (statistical effect). The contradiction of small sizes and large species richness in the Eocene might be explained by the fact that cosmopolitan species tend to stay small (Parker et al., 1999). Hence, a large number of cosmopolitan species, as in the Eocene, would not have the ability to produce a large size$_{\text{assemblage5}}$.

This condition changed with the beginning of cooling in high latitudes starting around 50 Ma (Zachos et al., 2001) and the onset of major glaciation in the Southern Hemisphere around the Eocene/Oligocene boundary (Miller et al., 1987). Subpolar surface-water temperatures had decreased by about 12 °C since the Late Eocene (Shackleton, 1984), whereas those from equatorial latitudes had hardly changed at all. Around 43 Ma, the build-up of ice on Antarctica had started with mountain glaciers reaching to sea level (Ehrmann and Mackensen, 1992). Large continental ice sheets were established around 34 Ma (Shackleton, 1986; Zachos et al., 1994), although global deep-sea temperatures did not change at this time (Lear et al., 2000).

The late Middle Eocene through early Oligocene is characterised by a transitional fauna. Early Eocene species, which were adapted to stable environmental conditions, became extinct and new species evolved, which had the ability to survive the changing environmental conditions (Keller et al., 1992). The large number of extinctions from the middle Eocene though to the middle Oligocene peaked around the Middle/Late Eocene and Early/Late Oligocene boundaries (Keller et al., 1992).

In the late Middle Eocene (Bartonian), our data show a divergence in the size of foraminiferal assemblages in high and low latitudes (Fig. 5.3 and 5.7). The Mid-Eocene shows the highest rate of appearance of new genera in the Tertiary (Tappan and Loeblich, 1988). The surface dwelling morozovellids, acarininids and globigerinathekids did not survive this change (Boersma et al., 1987) and the number of species dwelling at intermediate depth increased. Additionally, tropical and subtropical faunas in mid latitudes were replaced by cool and temperature assemblages in the Mid-Eocene (Keller et al., 1992). The evolution of distinct faunas in low and high latitudes is also considered responsible for the divergence of planktic foraminiferal assemblage sizes in the two environments.

Boersma & Premoli-Silva (1987) related the changes in Paleogene foraminiferal diversity and population structure to changes in oceanic productivity and the depth of the thermocline. They explained low diversity, extinction of thermophilic species, and the dominance of opportunistic, subeuphotic and temperate species as a result of cooling and eutrophication from late Middle Eocene to Mid-Oligocene. This is consistent with the reported increase in the number of species dwelling at intermediate depth and the evolution of deep dwelling species (Keller et al., 1992), which depend on a larger export production to thrive upon.

Our $\Delta\delta^{18}0_{\text{benthic-planktic}}$ comparison does not show an increase in temperature gradients in the extratropical areas during the significant increase in $\text{size}_{\text{assemblage5}}$, which started around 42 Ma. The suggestion of Boersma et al. (1987) that productivity influenced the structure of foraminiferal communities in the early Paleocene and from the late Middle Eocene through Mid-Oligocene, thus is consistent with the remarkable correlation of $\text{size}_{\text{assemblage5}}$ with $\delta^{13}C$ at theses times. The “transitional phase” with intermediate $\text{size}_{\text{assemblage5}}$, which started in the Mid-Eocene at low and intermediate latitudes, lasted through the Oligocene to the Mid-Miocene.

5.4.4 Oligocene

Around the Eocene/Oligocene boundary, truly polar conditions were established at southern high-latitudes (Kennett and Barker, 1990). This was accompanied by the formation of Antarctic Bottom Water, the initiation of Circum-Antarctic Current (Kennett and Barker, 1990) and large-scale glaciation on East Antarctica (Ehrmann and Mackensen, 1992). The development of the cold Circum-Antarctic Current also led to well-defined cold currents in the eastern parts of the transitional and subtropical ocean basins of the southern hemisphere which carried high latitude fauna northwards, e.g. along the western Coast of Africa to DSDP 366 (Fig. 5.2). As a counterbalance, warm currents brought subtropical fauna southwards (Jenkins, 1985), e.g. along the east coat of South America to DSDP Site 516F (Fig. 5.2). This explains the different Neogene size pattern of these two cores despite their very similar latitude.

Cooler high latitude temperatures, may have enabled the development of a pycnocline and a denser, more discreet chlorophyll maximum seems to parallel selective extinctions of surface dwelling groups (van Eijden, 1995), whereas forms at intermediate and greater depth were not affected and diversified. Long ranging, specialised, morphologically diverse forms were eliminated at all latitudes (Boersma and Premoli Silva, 1991; Banerjee and Boyajian, 1997). The Early Oligocene was characterised by low diversity (Bolli et al., 1985, see figure 5.6). As identified by isotope analysis, assemblages were dominated by deep dwelling taxa and surface dwelling species remained rare, in the >250 µm fraction in the Early Oligocene (van Eijden, 1995).

In general, size changes do not correlate well with paleo-temperature in this interval. The size trends more closely follow $\delta^{13}C$ variability in the latest Eocene to earliest Miocene (Fig. 5.5b). Export production was interpreted to have increased by a factor of 2 to 3 at the Eocene-Oligocene transition (Miller et al., 1987). The inferred increase in food supply from the photic zone started in the Late Eocene (Diester-Haass and Zahn, 2001) and led to a diversification of niches in the deeper parts of the upper water column allowing these deep-dwelling taxa to attain larger sizes.

The latitudinal thermal gradients weakened in the Late Oligocene due to a global warming (Lear et al., 2000; Zachos et al., 2001) starting around 26-27 Ma. At 27 Ma, the sizes in high and low latitudes show a decrease to Paleogene values (Fig. 5.3), possibly as a result of reduced vertical and latitudinal temperature gradients. As a consequence of decreased meridional temperature gradients, biogeographic provinces broadened, became fewer in number and planktonic foraminiferal faunas became more generalised (e.g. Cifelli, 1969; Kennett, 1978). Although the biogeographic ranges of many species expanded, important differences remained in diversity and composition between low and high latitudes (Leckie et al., 1993), which is also evident in the $\text{size}_{\text{assemblage5}}$ differences (Fig. 5.3). The warming trend led to a change in the assemblage composition due to an increased number of warm-water surface dwellers (Keller et al., 1987). This reoccupation of near surface environments should have increased the number of temperature dependent species at the expense of nutrient dependent ones. Hence, the system may have swung back from a nutrient dependent to a temperature dependent one. And indeed, from the Late Oligocene on, changes in planktic foraminiferal assemblage sizes in low latitudes and paleo-temperatures derived from both Mg/Ca and $\delta^{18}0$ proxies parallel each other.

5.4.5 Miocene

Beginning at the end of the Miocene climatic optimum 18 to 17 Ma ago (Savin et al., 1975; Shackleton and Kennett, 1975), the latitudinal temperature gradient increased. Between 16 to 14 Ma, the steepened latitudinal temperature gradient caused an increase in stratification (Loutit et al., 1983). The trend of latitudinal differentiation of foraminiferal faunas, which started in the Oligocene, continued and intensified in the Miocene (Kennett, 1977). This trend is evident from the increasing number of species (Fig. 5.6) (Bolli et al., 1985; Wei and Kennett, 1986). In contrast to the Oligocene assemblages, which were uniformly distributed over large latitudinal ranges, numerous distinct latitudinal provinces evolved during the Neogene (Kennett et al., 1985). Additionally, the composition of the assemblage changed from a fauna dominated by surface dwellers in the Early and Mid-Miocene, to a more equitable distribution of surface, intermediate and deep dwellers in the Late Miocene. This was caused by the development of a major intermediate-water planktonic foraminiferal assemblage, with new forms mainly originating at low latitudes (Keller, 1985; Wei and Kennett, 1986) (see also Fig 5.6). Wei and Kennett (1986) assumed that this diversification was stimulated by newly developing ecological niches.

In the Miocene, high and low latitude assemblages started to diverge more strongly than ever before. Hence, the distinct size increase of subtropical and tropical planktic foraminiferal assemblages and the Miocene diversification (Wei and Kennett, 1986) were likely responses to an increase in the thermal gradients and the related subdivision of surface water masses. The increase in vertical niche partitioning at low-latitudes enabled planktic foraminifers to grow to unprecedented sizes by the end of the Miocene. By 10 Ma, $\text{size}_{\text{assemblage5}}$ had reached values, which had last prevailed in the Maastrichtian. The distinct cooling in the mid- and high-latitudes around 6 to 6.5 Ma, which additionally strengthened the oceanic latitudinal and vertical thermal gradients, furthered habitat stratification, and led to new intermediate waters niches (Wei and Kennett, 1986). By the end of the Early Miocene diversification, the Eocene range of bauplan was essentially re-established (Norris, 1991).

5.4.6 Pliocene/Pleistocene

Additional cooling and ice-sheet expansion (Kennett and Barker, 1990) continued until the earliest Pliocene. Around 4.6 – 2.7 Ma the Panama seaway closed (Duque-Caro, 1990; Haug and Tiedemann, 1998), after several million years of progressively restricted oceanic circulation (Duque-Caro, 1990). The Pliocene Climate Optimum (3.2 Ma) was followed by decreasing $\delta^{18}0$

values in benthic foraminifers characterising the onset of major Northern Hemisphere glaciation (Shackleton et al., 1988). Since 2.7 Ma, pronounced glacial-interglacial cycles are documented in the geological record. All these environmental changes may have affected planktic foraminiferal test size and future work should focus on these possible interactions.

The shoaling of the thermocline persisted though the Pliocene when increases in the abundance of a new set of shallow, intermediate and deep-dwelling species of planktic foraminifers coincided with the closing of the Panamanian Seaway. The onset of Pleistocene glacial-interglacial cycles, affected both surface and deeper water species, seemingly at random (Chapman, 2000). Extinctions, affecting 40% of the taxa, took place over an 800ky interval without clear evidence of preferential extinction in any regions (Chapman, 2000). These changes are not a result from adverse interaction with newly evolved species, but they were rather related to abiotic changes within the environment which presumably exceeded ecological thresholds. During this time interval both assemblage size at Ontong Java and species size in the equatorial Indian Ocean decreased for a short period of time (Fig. 5.9). From 2.5 Myr to present, unprecedented thermal gradients coincide with unprecedented planktic foraminiferal sizes in areas with high stratification.

Thanks to a few morphological studies of single lineages (Malmgren et al., 1983, Biolzi, 1991), assemblage sizes and single lineage size can be compared in the Pliocene/Pleistocene interval. The size within the *G. tumida* lineage (Malmgren et al., 1983) is parallel to $\text{size}_{\text{assemblage5}}$ and to the oxygen isotopes (Fig. 5.9). Around the Miocene/Pliocene boundary, $\text{size}_{\text{assemblage5}}$ increased in several cores (Rio Grande Rise, Exmouth Plateau, Ceara Rise, Fig. 5.2). This increase is also documented in the *G. tumida* lineage (Malmgren et al., 1983, Fig. 5.9) and in *Neogloboquadrina dutertrei* and *N. humerosa* during the past 5 Myrs (Biolzi, 1991). These changes can be attributed to changes in the vertical water mass structure (Malmgren et al., 1983). Changes in the late Neogene assemblage-size and species-size are also closely correlated, as observed in the Paleocene. Hence, we assume that environmental change acts at several levels: the group, the genus with species of similar adaptations and the population of the species and its ontogeny. This is not just true for low-latitudes records, but better adaptation of *N. pachyderma* also led to an increase in test size in the Norwegian-Greenland sea during the last 1.3 Myrs (Huber et al., 2000).

5.5 THE DEBATE ON DIRECTIONALISM VERSUS VARIANCE INCREASE

What is the reason for $\text{size}_{\text{assemblage5}}$ changes over time? A similar question was posed by Stanley (1973): why do iterative radiations start with small sizes (Stanley, 1973)? He suggested that larger species might prevent evolutionary transitions between major adaptive zones. Hence, perturbations leave the smaller generalists behind, who are better able to cross adaptive barriers and subsequently can establish new lineages.

Unspecialised smaller species, thus, have the structural flexibility to found new lineages. Larger species need more complex and specialised structures to perform the same surface/ volume related task as their smaller relatives do (the principle of similitude Thompson, 1917). This is based on the size dependent relationship between surface area, which grows with the square, and volume, which triples at a given growth rate. Large size may not be universally advantageous, due to size dependent scaling of metabolic rates and foraging. Consequently, large size may be inhibitory to speciation (Arnold et al., 1995) and larger sized taxa, which are very specialised, may be more prone to extinction (Norris, 1991). The most conservative foraminiferal morphology is the simple trochospiral unornamented stock (Frerichs, 1971), which was the dominating morphotype after major species richness reductions in the earliest Paleocene and the early Oligocene. For growth towards large sizes, high food supply (i.e. productivity) and pronounced vertical temperature gradients seem a necessary prerequisite to sustain a larger body volume. liability

What are the possible advantages of becoming large? Benefits may include an improved ability to capture prey, the possibility to ward off predators, greater reproductive success, and a better regulation of the internal environments (Stanley, 1973; Calder, 1984). Larger species in the Holocene are either intermediate to deep dwelling or symbiont bearing species. Innovations, such as gigantism, may allow invasion of new adaptive zones (in this case a depth habitat), increased fitness, a larger number of offspring or ecological specialisation (Heard and Hauser, 1995). Deeper dwelling forms have greater geographic ranges (Lazarus, 1983), which might make them less vulnerable to climatic change. We also need to ask what the advantages of small size might be, which some species, such as the globigerinid forms, seem to have chosen.

5.5.1 Evolutionary models

Many ideas regarding the interpretation of the fossil record with respect to the mechanisms of long-term evolution have a long and contentious history. A first issue is that it is unclear if large-scale evolutionary trends result from either active driving forces, i.e., may be directional, or from passive diffusion in bound spaces, i.e., increase in random variation (McShea, 1994). Shifts in size or complexity can be driven by active migration or adaptation to a more favourable habitat, innovations by advantageous adaptation to existing conditions or by passive diffusion such a dispersal (McShea, 1994).

Analyses of changes in minimum sizes within a distribution enable us to test for directional size changes versus a simple increase in variance. Increase in variance should keep a constant minimum size, whereas an active trend should increase both minimum and variance (McShea, 1994). Since our size spectra have artificial minimum sizes due to the sieving procedure, we cannot directly test these hypotheses.

A second issue is the relative importance of biotic versus abiotic controls on evolutionary change, exemplified by the contrasting Red Queen hypothesis (van Valen, 1973) and the stationary model (Stenseth and Maynard Smith, 1984). The first predicts that a homogenous group of organisms is forced to evolve as a consequence of random biotic interactions even in the absence of physical environmental change. The latter suggests that evolution was largely driven by abiotic changes, and would have slowed down during periods of physical quiescence. While the Red Queen hypothesis is based on intrinsic biotic interactions causing evolution (van Valen, 1973; Sepkoski, 1978), the stationary model requires a correlation to specific environmental driving forces. A third possibility is an intrinsic trend for simple increases in variance over time (Gould, 1988; Norris, 1991, Jablonski, 1997).

The Cenozoic record of foraminifers suggests that this group underwent repetitive increase in diversity, morphological complexity and changes in the distribution (Lipps, 1970). We have demonstrated that planktic foraminiferal size changes show a relationship to environmental changes, such as temperature, surface water stratification and fertility, as well as to other morphological characters and species richness. Hence, our data clearly support the stationary model.

Among the potential driving forces are changes in circulation patterns, vertical structure and stability of the surface water, thermocline depth, latitudinal gradients, rates and loci of upwelling, bottom water formation, and supply of nutrients (Wei and Kennett, 1986). Environmental change leads to changes in the configuration and quality of habitats. New selection pressures would result from these changes, causing the reorganisation of the fauna.

Biotic processes may also have played a role and included the mutational breaching of adaptive thresholds and changes in trophic relationships, competition, resistance to viral infections and other factors.

The most favoured abiotic parameter related to foraminiferal evolution is temperature (Berggren, 1969; Cifelli, 1969; Lipps, 1970; Frerichs, 1971). Lipps (1970) assumed that the iterative evolution of foraminiferal morphology was controlled by an adaptive threshold related to depth stratification of the water column. Douglas and Savin (1978) provided stable isotopic support for this model. As a consequence, planktic foraminiferal diversity might be connected to changes in the structure of the surface water rather than to temperature *per se* (Vincent and Berger, 1981). We documented here that a similar process acted on $\text{size}_{\text{assemblage5}}$. Cooling of the polar areas led to changes in the thermocline structure and its position relative to the euphotic zone and the position of the chlorophyll maximum (see Chaisson and Leckie, 1993 for discussion of these changes on diversity).

5.5.2 The stationary model: habitat heterogeneity

Lipps (1970) was not the first to recognise the importance of changing temperature gradients for the iterative evolution of planktic foraminifers. Ciffeli (1969) first related the iterative patterns to major changes in the dynamic structure of surface waters. He suggested that an uniformly cool ocean with degraded thermal barriers caused a reduction of morphological diversity. Lipps (1970) emphasised the relative importance of the vertical temperature gradients in addition to the horizontal ones for species maintenance and diversification. In contrast to Ciffeli (1069), he related a low diversity to warm climates, where thermally related mechanisms for species maintenance are eliminated, whereas cool polar temperatures intensify the thermal mechanisms which cause an increase in the number of species. We fully support the Lipps hypothesis because increases in $\text{size}_{\text{assemblage5}}$ are related to strengthening of temperature differences (Fig. 5.7). In areas without strong surface water stratification, e.g. high latitudes, large sizes are never obtained during the entire Cenozoic (Fig. 5.7).

Oceanic stratification allows foraminifers to invade different levels of the water columns (Lipps, 1970; Douglas and Savin, 1978; Hart, 1980; Lazarus, 1983). An increase in habitat stratification thus provides more ecological niches (Wei and Kennett, 1986). In times with a strong stratification, intermediate water habitats have been exploited (Douglas and Savin, 1978). Specialised foraminiferal species tend to become large, whereas cosmopolitan generalists tend to be small (Arnold, 1983). Consequently, increases in stratification should lead to both diversification and an increase in size ranges. Warm polar temperatures cause a loss of niches, lead to global occurrences of species, small geographic size differences and small sizes.

Habitat heterogeneity permits radiations (Ciffeli, 1969; Lipps, 1970; Douglas and Savin, 1978; Hart, 1980; Lazarus, 1983; Wei and Kennett, 1986; Norris, 1991). It is assumed that the iterative homeomorphy was associated with the development of forms that inhabited deeper parts of the water columns. Increased stratification, whether related to a thermo- or pycnocline, fosters the formation of a deep chlorophyll maximum. Development of density surfaces also increases reproductive success, since the gametes are forced to stay in a rather discrete part of the water column which might provide additional possibilities for speciation (Hemleben, pers. com. 2001). Hallock (1987) pointed out that high species diversity is promoted by the combined development of eutrophic and oligotrophic conditions in different parts of the ocean. As a consequence of this heterogeneity, evolutionary adaptations may have become more specialised and species more provincial (Lipps, 1970). A loss of habitat heterogeneity, as in the earliest Paleocene (D' Hondt et al., 1998) and Oligocene (Cifelli, 1969), favours generalists.

5.5.3 Analysis of macroevolutionary data sets on foraminifers

Several independent data sets point to a relationship between foraminiferal evolution and the thermocline structure. Lipps (1970) based his hypothesis on species richness within several groups of foraminifers (Fig. 5.11), whereas Cifelli (1969) compiled data about the iterative appearance of morphogroups of foraminifers (Fig. 5.12).

We presented a record of size changes in planktic foraminiferal assemblages. Surprisingly, these data sets do not show the same macroevolutionary pattern over time (see also Fig. 5.6). Despite high species richness in the Eocene, $\text{size}_{\text{assemblage5}}$ are rather small. In contrast, during the low diversity interval in the Oligocene, intermediate $\text{size}_{\text{assemblage5}}$ has been measured.

Morphological diversity (Ciffeli) and species richness (Lipps) show similar patterns, which is not surprising given that the division of species is based on morphological criteria.

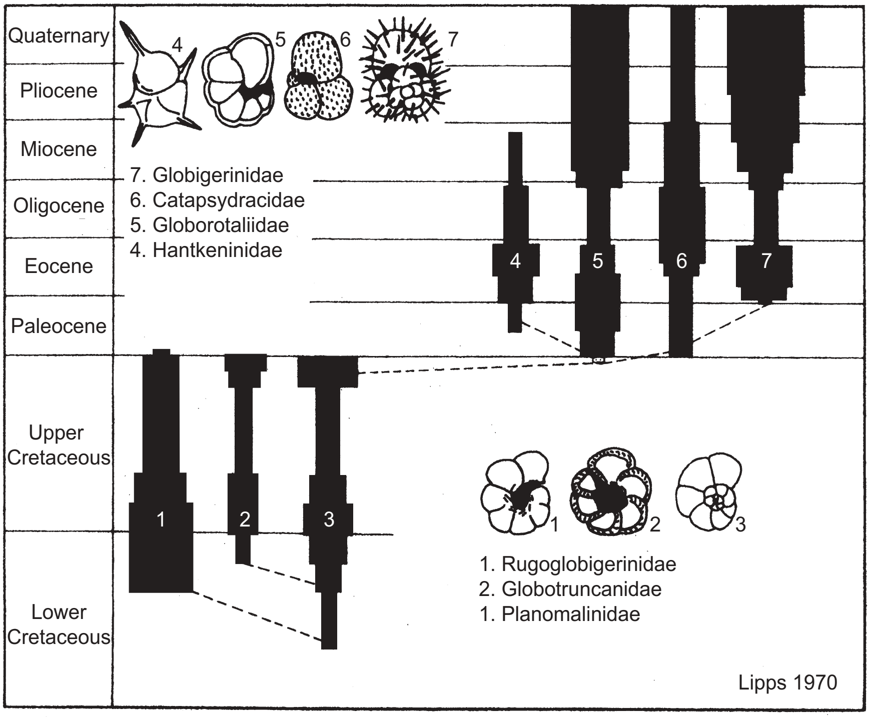


Figure 5.11: Iterative evolution of species richness for different families of planktic foraminifers from the lower Cretaceous till Recent (Lipps, 1970).

There are two potential explanations, first, that environmental change may have acted differently on the two or through time or both, and secondly the global diversity curves might not display the real assemblage diversity.

During the Paleocene and Eocene more complex forms with acute and keeled peripheries contribute to the assemblage diversity than in the Oligocene. Before and after the Oligocene, planktic foraminiferal assemblages showed pronounced latitudinal endemism (Lipps, 1970). Oligocene fauna was simple and world-wide in occurrence. The mid-Eocene to mid-Oligocene diversity loss was caused by a reduction of surface dwellers (Keller et al., 1992), a likely consequence of cooling temperatures in the surface water. Some of the globigerinids, which produced the largest species in the Oligocene, were adapted to deeper water and survived the species reduction.

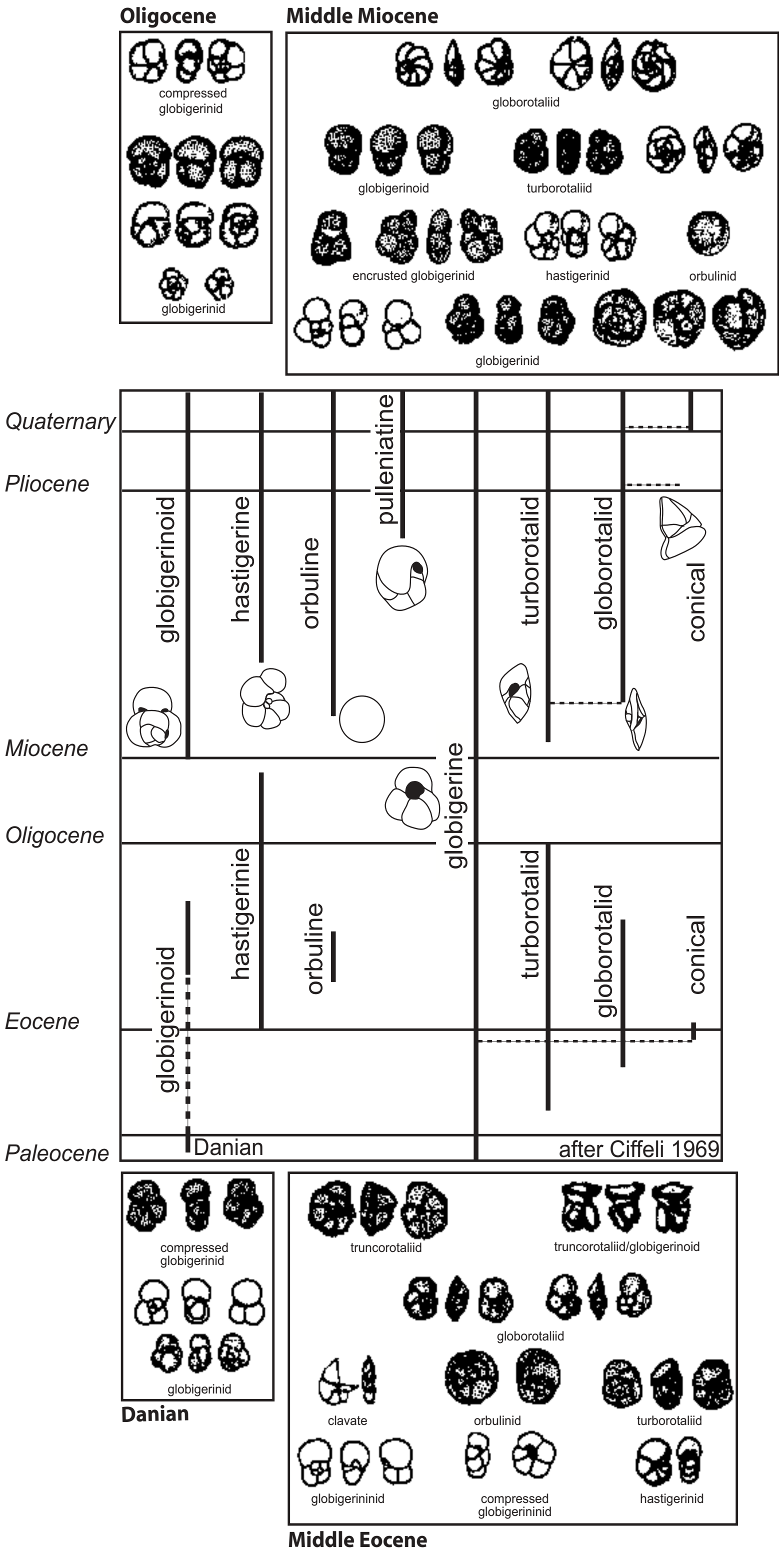


Figure 5.12: Iterative evolution of morphotypes during the Cenozoic (after Ciffeli, 1969). Overviews about morphological variability in selected time intervals: Danian, Middle Eocene, Oligocene, Middle Miocene from Vincent and Berger (1981).

One example for the lack of correlation between diversity and size patterns is the Oligocene. The change in species composition led to a global “upwelling fauna” (Hallock, 1987). Nutrient rich waters are characterised by high abundance of few species with simple morphologies (mostly spinose, opportunistic globigerinid-form forms) (Boersma and Premoli-Silva, 1991). This faunal evidence combined with sedimentary records, which display increase productivity (Wagner, in press), indicate that planktic foraminifers assemblage size increased in the Late Oligocene were related to changes in productivity. It thus appears that during the Oligocene planktic foraminiferal sizes changes little, while species richness is reduced.

It seems expedient, however, to emphasise here the difficulties inherent in compilations of diversity data. Existing compilations show significant differences in species richness in the Neogene, dependent on the original range charts used (Thunell, 1981), (Wei and Kennett, 1986) for the Neogene, (Norris, 1991) based on Kennett and Srinivasan (1983), Tourmarkine and Luterbacher 1985) and by Beckmann based on Bolli et al. (1985) differ from each other. Thunell’s (1981) and the compilations of Bolli et al.’s (1985) range charts show a continuous increase in diversity in the Neogene, whereas those of Wei and Kennett (1986) and those based on Kennett and Srinivasan (1983) result in a decline in species richness since the latest Miocene. Thunell (1981) determined very low species richness in the Eocene around 50 Ma, which is not evident in any of the other compilations. All of these are based on stratigraphic literature, and hence emphasise stratigraphically important species. Therefore, the possibility exists that a new compilation of species richness for well-preserved samples might lead to another result. Species richness determination from geological samples may have another problem. Molecular genetic studies of living planktic foraminifers have shown that conventional species often include two or more genetically distinct taxa (Huber et al., 1997; Norris, 2000; Vargas et al., 2001). Traditional taxonomic efforts may have concentrated preferentially on lineages that have evolved rapidly leaving conservative species underrepresented (Pearson, 1998). Lineages might have been split into a series of morphotypes that are accorded status as taxonomic units event though they may never have been genetically isolated biological species (Pearson, 1992). The rather simple morphologies in the Oligocene (Fig. 5.12) could lead to a “undersplitting” of morphotypes in comparison to species with more easily recognisable morphological differences, such as the keeled taxa in the Eocene.

5.5.4 A key innovation: the unprecedented size increase in the late Neogene

What factors allowed foraminifers in the last 10 My to reach sizes they never achieved before? Was there anything special in the paleoceanographic situation of the Neogene? Pronounced polar cooling may have led to ecological niche separation at two distinct spatial scales. The position of thermocline, deep chlorophyll maximum may have migrated vertically over dozens to a few hundred meters. On the scale of hundreds to thousands of kilometres, latitudinal temperature gradients led to meridional provincialism (Thunell, 1981). Both effects probably contribute to high diversity and size in the late Neogene.

Quaternary temperature gradients and climatic zonation is at an all-time high (Jablonski et al., 1985). Continental masses are fragmented leading to oceanic provincialism and allowing for allopatric speciation (Jablonski et al., 1985). Strong vertical temperature gradients will increase the potential of depth parapatric speciation (Lazarus, 1983). Furthermore, increased seasonality fostered by cooling and monsoonal effects may promote seasonal parapatry (Norris, 2000)

Benthic foraminifers (Kaiho, 1998) also show repetitive developments to larger sizes (Fig. 5.13). In benthic foraminifers, as in planktic foraminifers, the fast changes are made possible after sudden reductions in sizes and species richness.

The Cenozoic minimum in size of benthic foraminifers is related to the extinction event in the Late Paleocene Thermal Maximum. Exceptionally larger sizes evolved in the latest Eocene, slightly later than in the size increase of the planktic foraminifers. Kaiho (1998) assumed that small sizes are related to dysoxic conditions, enhanced carbon flux, or decreased ventilation. Assuming that dissolved oxygen was driving the benthic size record is too simple, since there is no indication for low oxygen conditions in the Miocene and Pliocene (Kaiho, 1998). The Neogene size increase of planktic and benthic foraminifers above the Cenozoic average happened in a time of enhanced accumulation of organic matter (Wallmann, 2000; Wagner, in press). Hence, the long-term size increase of benthic foraminifers might also have been influenced by productivity, as it has been documented within the Pleistocene for *Melonis barleanum* (Caralp, 1989). The detailed forcing of size increases observed in various groups of protists must remain speculative at present, because of limited temporal and spatial samples resolution. It appears evident, however, that major global climatic changes probably controlled not only extinctions and speciations but also the sizes of protists in the surface waters and the deep sea.

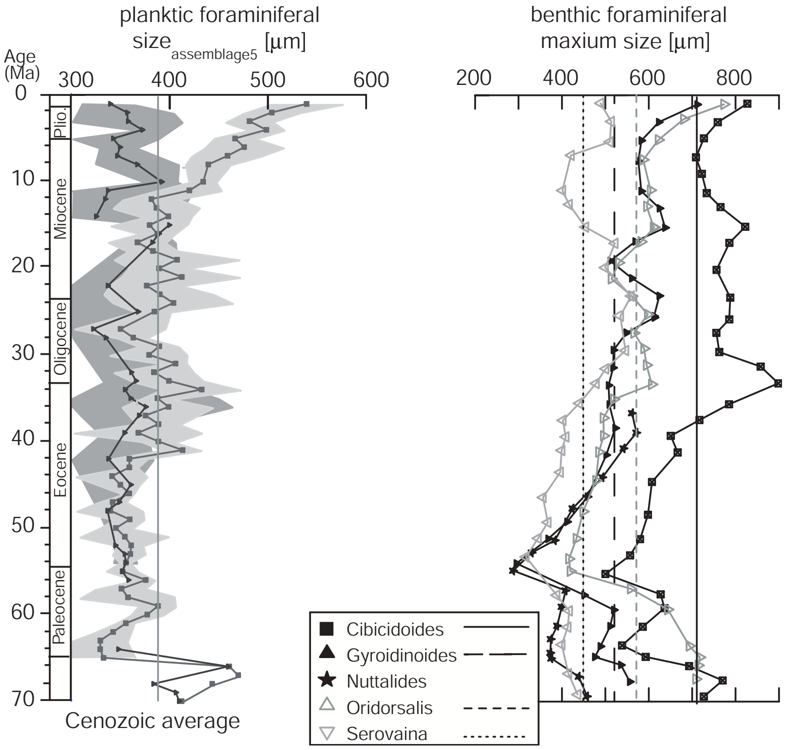


Figure 5.13: Size$_{\text{assemblage5}}$ of high latitudes (subpolar to temperate cores) and low latitudes (subtropical and tropical) comparing benthic foraminiferal maximum size of *Cibicidoides*, *Gyroidinoides*, *Nuttalides*, *Oridorsalis*, and *Serovaina* (Kaiho, 1999). The shaded area within the size data represents one standard deviation from the mean of size$_{\text{assemblage5}}$ for high latitudes (dark grey) and low latitudes (light grey). The grey line represents the Cenozoic average of the entire data set.

5.5.5 Absence of size increases at high latitudes

Assemblages in high latitudes are unlikely to have experienced environmental conditions during the past 65 Myrs that enabled them to grow to large size. These pervasive moderate to small sizes appear consistent with the absence of continued strong stratification, seasonal stress and low diversity. The diversity in this regions is low, and may inhibit the potential for evolution of large sized species. Quaternary species in high latitudes also are the most cosmopolitan and tend to occur in areas with strong seasonality. The high energetic cost of surviving seasonal extremes may preclude speciation and growth to large size (Parson, 1992).

5.6 SUMMARY AND CONCLUSIONS

1. The size record of planktic foraminifers in the Cenozoic can be divided into three different intervals, the time of growing dwarfs from the K/T boundary to the Late Eocene, a transition period from the Late Eocene to the Mid-Miocene, and a time of growth to gigantism from the Mid-Miocene to Recent.
2. A pronounced Neogene size increase is observed in all of the studied warm-water sites, whereas high-latitude faunas display stability. The large sizes of warm water Holocene planktic foraminiferal assemblages are unprecedented in the geological record.
3. In the early Paleogene, foraminiferal assemblage sizes are similar at all latitudes indicating a lack of provincialism. In the middle Eocene, high latitude and low latitude assemblage sizes decouple, probably as a consequence of the steepening of the latitudinal temperature and vertical gradients related to high latitude cooling.
4. Fluctuations in the size of low diversity assemblages in the Paleocene and the Oligocene, which are reduced in the number of surface dwellers, seem correlated to productivity rather than temperature changes.
5. Throughout most of the Cenozoic, size and species richness increases seem to occur with increases in vertical water stratification in low latitudes and to polar cooling phases. The stratification results in an increase in the number of niches, which allows for a specific adaptation and consequently growth towards large size. Habitat heterogeneity is necessary to obtain large size.
6. The close relationship between size and environmental change leads us to favour the stationary model (Stenseth and Maynard Smith, 1984).
7. On a macroevolutionary scale, global climatic changes have apparently not only controlled extinctions and speciations but also the size of foraminifers in the surface waters and the deep sea.

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CONCLUSION AND OUTLOOK

Given the prominent role foraminifers have played in Mesozoic and Cenozoic global change research, it is surprising how little we know about the reaction of this group of microfossils to major environmental change. A prerequisite to study the effects of environmental perturbation on foraminifers is that biostratigraphic records are comparable across the taxonomic spectrum and throughout the entire stratigraphic interval. The investigation of morphology allows analysis of changes in foraminifers without grouping them in any way. Size change studies of entire assemblages have the advantage of being taxon free and avoiding bias of any kind of grouping. Additionally, the analyses of entire assemblages enables investigation of possible long term and global processes.

All data sets consistently show that 1) climatic change is a driving force in size changes, 2) the partitioning of the surface wates and heterogeneity of niches allows growth to large size and 3) temperature alone is insufficient to explain the observed pattern, which requires a combination of temperature, fertility and environmental stability. We follow Ciffeli (1969), Lipps (1970) and Norris (1991) in concluding that foraminiferal test forms, size and shape, are prominent targets of natural selection. We showed that the present might not be the key to the past, since the size range in the Late Neogene is unprecedented in the past 70 Myrs. The most comparable size range to the Neogene was previously observed in the Maastrichtian.

The size variation of foraminifers might help to improve our understanding of the interrelationship of evolutionary processes and ecology with rates, magnitudes and spatial scales of change in the physical and biotic environment. It is an important goal, in times of man-made global climate change, to understand the consequences of environmental changes on the marine biota. A multidisciplinary approach, combining high-resolution geochronology with morphological change, evolutionary studies at different levels, isotope analyses and quantification of the regional change in carbon accumulation will help to elucidate interactions between the biosphere and climate. In the literature, physico-chemical proxies such as changes in the amount of sand fraction and carbonate accumulation are used to investigate paleoceanographic changes, but the biotic impact on these variations is ignored. The size increase of foraminifers might lead to a larger amount of sand and carbonate accumulation. The analysis of foraminiferal size change might add understanding of the biological impact on these processes.

A) PALEOCEANOGRAPHIC INSIGHTS BY REFINED PATTERNS OF SIZE CHANGES COMBINED WITH ISOTOPE ANALYSIS: THE NEOGENE

There is a general need to increase our understanding of the rate and mode of foraminiferal size change in the Neogene. Are the hitherto identified planktic foraminiferal test size increases gradual or did they happen as regional or global steps? An improved chronology of these size increases is necessary to understand if these changes in size are gradual or step-wise. If there are general similarities between regions as indicated by this study, are these events synchronous or diachronous in different basins?

Based on a better knowledge of the mode and timing of the change, we have to understand the relationship between macro- and microevolution. Are the low-latitude size increases observed in all taxa or only in a few? Assemblage size changes can be a response to macro- or microevolutionary changes. Macroevolutionary changes might be related to major radiations or modifications, such as global diversifications. Alternatively, intraspecific size changes influence the assemblage size. During times of major assemblage size change, the taxonomic composition of the assemblage and the size spectra of dominant species should be analysed to disentangle the effects of changing species composition from those of intra-specific size change. Changing size spectra of morphotypes might be related to two different mechanisms, either ecophenotypic size variations or size changes associated with speciation events. Size changes alone may not help to identify speciation events. Combining size and shape analyses of species will help to elucidate if these size variations are related to adaptation or speciation.

The more detailed pattern of size changes might provide better insights into the influence of paleoceanographic changes on size. How closely are assemblage or species size changes related to changes in the thermocline structure? Changes in surface-water stratification can be recognised by changes in the $\delta^{18}0$ and $\delta^{13}C$ gradients between surface and thermocline dwelling species. This thesis cannot not answer this question, since high resolution comparisons of size and isotope measurements from the same samples are necessary to understand the mechanism behind this higher amplitude fluctuation. Isotope analyses have to be performed to verify the relationship between changing habitats (water-mass structure) and size change.

B) EXTREME WARMTH, STRATIFICATION CHANGES AND ANOXIC EVENTS: THE CRETACEOUS

When compared to present, the Cretaceous was a time of high global temperature with a low thermal gradient between the poles and the tropics. The most prominent feature of the Cretaceous is the occurrence of Oceanic Anoxic Events (OAE,) the most important of which are the Selli level (OAE 1a) in the Aptian and the Bonarelli event (OAE 2) at the Cenomanian-Turonian boundary.

Planktic foraminiferal species during the Selli event decreased in richness and abundance (Premoli-Silva, 1999) without any turnover of species. A reduction of foraminiferal size is described. The Bonarelli event in contrast, displays a massive extinction of specialised deep-dwelling species and a proliferation of opportunistic species (Premoli-Silva, 1999) without a major change in diversity. This event is also characterised by a reduction in size (Nederbragt, 1999). The cause for the extinction of the deep-dwellers is thought to be a breakdown in the vertical structure of the surface waters at steady sea surface temperatures (Huber et al., 1999). This possibly would allow testing of the hypothesis that the structure of the water column is more important than temperature per se for the sizes in foraminiferal assemblages. During reductions in species richness in the Cenozoic, surface-dwelling species become preferentially extinct in contrast to deep-dwellers during the Cretaceous. Hence, the potential difference in size development might add further information about the importance of the habitat structure for the assemblage size.

The thermal maximum of the last 120 Myrs is assumed to be in the Turonian (Huber et al., 1999). Global temperature gradients were minimal (Huber, 1995) and stratification varied strongly over time (Norris, 2000). Erbacher et al. (2000) proposed an inverse stratification in the Atlantic during the OAE 1b, whereas Wilson (2001) suggests no stratification and stagnation for the OAE 1d. Consequently, the Cretaceous would be a perfect time to test influences of stratification on sizes in planktic foraminiferal assemblages.

C) SIZE VARIATION DURING THE TIME OF ORIGIN: THE JURASSIC

Foraminifers evolved during the Cambrian as benthic organisms. During the Jurassic, foraminifers started to explore and calcify in the upper surface waters. The rise in planktic foraminifers is assumed to be a consequence of warm, stratified and poorly oxygenated water (Loeblich and Tappan, 1970). The cause of the expansion of variance in diversity and the relationship of diversity and size during their origin is an open question. This problem is challenging, since the abundance of planktic foraminifers was low and the numbers of benthic individuals high. Hence, size analysis in this time interval must be combined with automated recognition systems and a neuronal net has to be trained for this interval.

D) EXTREME EVENTS: THE LPTM

It is interesting to apply the newly gained knowledge to times of rapid climate change, such as the Late Paleocene Thermal Maximum (LPTM). This environmental aberration coincides with a massive size reduction and the largest extinction event in benthic foraminifers. It is known as an episode of abrupt global warming (Bains et al., 1999), with a 5-6°C rise in bottom waters (Kennett and Stott, 1991) and an 8°C rise in high latitude surface temperatures (Kelly et al., 1996). The planktic foraminifers reacted with a widespread proliferation of exotic planktic foraminiferal taxa (Kelly et al., 1996). The size analysis of Blake Nose displays a large variability in size during this event (Chapter 5). A high resolution study of size changes during the LPTM would be required to analyse the effect of aberrations on the planktic environment.

E) BIOLOGICAL INFLUENCE ON THE CARBON CYCLE: INSIGHT FROM FORAMINIFERS

An increase in size of one of the major carbonate producers - planktic foraminifers- (Schiebel, in press) in the pelagic realm could have an influence on carbonate accumulation. Hence, changes in foraminiferal test size may be related to changes in oceanic carbonate deposition rates and could be important for the global carbon cycle. Variations in foraminiferal test size affect the amount of carbonate precipitated. Consequently, carbonate precipitation provides strong feedback on the CO_2 budgets of the ocean/atmosphere system. Changing export production of carbonate to the deep sea will influence the depth of the carbonate compensation depth. Are changes in foraminiferal size related to the documented variation in the carbonate compensation depth?

On the other hand, the ability of foraminifers to calcify might be related to carbon supersaturation (Chapter 3). Pearson and Palmer (2001) described a lower pH in the Paleogene. More acid conditions would inhibit calcification. A reduced export of foraminiferal carbonate due to small sizes (Chapter 5) would increase the carbon reservoir of the ocean and also lead to a higher alkalinity, as described by Pearson and Palmer (2001). This possible relationship should be investigated in more detail. A prerequisite would be a better resolution of boron isotopes and, ideally, a combination of size and isotope measurements in one core.

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